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Leptodactylid Frogs of
the Genus *Eleutherodactylus*
in the Andes of Northern Ecuador
and Adjacent Colombia

By

John D. Lynch

UNIVERSITY OF KANSAS
LAWRENCE 1981

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July 8, 1981

Leptodactylid Frogs of the Genus *Eleutherodactylus*
in the Andes of Northern Ecuador and Adjacent Colombia

By

JOHN D. LYNCH

*Professor, School of Life Sciences
The University of Nebraska, Lincoln, Nebraska 68588
Associate, Division of Herpetology
Museum of Natural History, University of Kansas
Lawrence, Kansas 66045*

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Editor: Robert M. Mengel
Managing Editor: Joseph T. Collins

Miscellaneous Publication No. 72
pp. 1-46; 22 figures; 8 tables
Published July 8, 1981

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INTRODUCTION

Although a prominent component of the fauna of most mesic environments in northwestern South America, the genus *Eleutherodactylus* is poorly represented in the pajonales (=subpáramos) and páramos of southern Colombia and northern Ecuador. Field work in these highland areas by the late James A. Peters and his associates and by individuals associated with the Museum of Natural History of the University of Kansas has yielded adequate altitudinal and geographic samples of eleutherodactyline frogs to permit ecological and systematic summaries of the frogs of this region. This study is the fourth in a series describing the *Eleutherodactylus* of Ecuador. The first (Lynch, 1979) treated the fauna of southern Andean Ecuador, the second (Lynch, 1980) summarized the fauna of the western Amazonian Basin, and the third (Lynch and Duellman, 1980) treated those faunas on the Amazonian slopes of the Andes in Ecuador.

The principal area under discussion extends from the Nudo de Pasto in southern Colombia south to the Desierto de Palmira in southern Provincia Chimborazo of Ecuador (about 2° S). Pajonale and páramo habitats within this area originally ranged in altitude from 3200 to 4800 m (Acosta-Solis, 1968) but now extend to lower altitudes where human activity has removed the high Andean forests (ceja andina) or replaced them with *Eucalyptus*. Seven species of *Eleutherodactylus* and one species of *Phrynoporus* are restricted to or primarily distributed within the pajonales and páramos. Six other species [*Eleutherodactylus chloronotus* Lynch, *E. leoni* Lynch, *E. supernatis* Lynch, *E. trepidotus* Lynch, *E. w-nigrum* (Boettger), and *Phrynoporus peraccae* Lynch] are species of the ceja andina and are occasionally found in those pajonales that abut the high cloud forests.

Most Andean *Eleutherodactylus* have

restricted distributions. Three of the species found in the Andes of northern Ecuador are exceptions. *Eleutherodactylus curtipes* (Boulenger) ranges from the Colombia-Ecuador border (ca 1° N) south to the Desierto de Palmira (ca 2° S) over an altitudinal range of from 2750 m to at least 4400 m. Its northern limit corresponds in an interesting and suggestive way with the political boundary of Colombia and Ecuador but in spite of the efforts of several collectors the species has eluded discovery in Colombia. The collectors instead find *E. buckleyi* (Boulenger) there, a close relative. *Eleutherodactylus buckleyi* is also found in extreme northern Ecuador but is distributed primarily in Colombia, in the Cordillera Central (to ca 4° N). The third widely distributed species, *E. unistrigatus* (Günther), generally occurs at lower elevations and in somewhat more xeric situations than *E. buckleyi* and *E. curtipes*. *Eleutherodactylus unistrigatus* occurs from the Nudo de Pasto in southern Colombia south primarily through interandean Ecuador to the vicinity of Riobamba. The general concordance of the southern termini of *E. curtipes* and *E. unistrigatus* coupled with the presence of a distinctive suite of eleutherodactyline south of the Desierto de Palmira led Lynch (1972a) to postulate a faunal break.

Lynch (1972a) suggested that *E. buckleyi* and *E. curtipes* were synonymous. That view is contradicted, however, by the sympatric occurrence of the two frogs over much of Provincia Carchi, Ecuador.

The other four species of *Eleutherodactylus* and the only species of *Phrynoporus* (*P. brunneus* Lynch) found in high altitude grasslands in northern Ecuador have small distribution areas. These *Eleutherodactylus* are *E. orcesi* Lynch, *E. thymelensis* Lynch, and two species named below.

ACKNOWLEDGEMENTS

My field work in Ecuador was supported by grants from the Committee on Evolutionary Biology at the University of Kansas (1967), the Watkins Fund of the Museum of Natural History, University of Kansas (1968), the Society of the Sigma Xi (1968), the Penrose fund of the American Philosophical Society (1970), and by the University of Nebraska Research Council (1970, 1977). Travel to museums was supported by the University of Nebraska Research Council. The following curators provided working space at their museums: S. Ayala, A. Grandison, J. Hernández, R. Heyer, C. Myers, R. Nussbaum, the late J. Peters, P. Ruiz, the late C. Walker, E. Williams, G. Zug, and R. Zweifel. A. Leviton and H. Marx loaned critical material. William E. Duellman provided many amenities and the full facilities of the Division of Herpetology at the University of Kansas over the duration of this study. Rita Ricaurte and Jaime Villa helped me with Spanish.

Tom Berger, Dave Cannatella, Pat Fritts, Tom Fritts, Bob Henderson, and especially my wife Marsha shared the disappointments, discomforts, and excitement of field work in Ecuador. Fernando Ortiz, the late Francisco León Rodríguez, and Eugenia del Pino of The Universidad Católica de Quito provided logistic support and encouragement in Ecuador.

MATERIALS AND METHODS

Terminology follows that of Lynch and Duellman (1980). I have examined 3151 preserved specimens of the eight species discussed in this paper including the type specimens of all names except *Hylodes lehmanni*. Throughout the text, specimens are identified by their catalogue numbers and the appropriate acronym for the museum collection, as follows: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; BM, British Museum (Natural

History), London; CAS-SU, California Academy of Sciences-Stanford University Collection, San Francisco; FMNH, Field Museum of Natural History, Chicago; ICN, Instituto de Ciencias Naturales, Museo de Historia Natural, Bogotá; KU, Museum of Natural History, University of Kansas, Lawrence; LACM, Los Angeles County Museum of Natural History, Los Angeles; MCZ, Museum of Comparative Zoology, Cambridge; MLS, Museo, Universidad de La Salle, Bogotá; MNHNP, Muséum National d'histoire Naturelle, Paris; MZS, Museo Zoológico della Specola, Fiernze; UIMNH, University of Illinois Museum of Natural History, Urbana; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, National Museum of Natural History, Washington; UVMP, Museo Parasitología, Universidad de Valle, Cali.

KEY TO ELEUTHERODACTYLINE FROGS IN PÁRAMOS OF SOUTHERN COLOMBIA AND NORTHERN ECUADOR

The key presented below will suffice to identify any eleutherodactyline frog encountered in páramo and interandean valley habitats from the Nudo de Pasto in Colombia (ca 1° 30' N) south to the northern edge of the Nudo de Azuay in Ecuador (ca 2° 30' S) even though some of the included taxa rarely penetrate páramos. Figures 1 and 2 are provided as aids to the key.

- | | |
|---|-----------------------------------|
| 1. Toes bear discs on ventral surfaces | 3 |
| ----- | Toes lack discs |
| 2. Adults less than 22 mm SVL; outer metatarsal tubercle about same size as inner metatarsal tubercle | 2 |
| ----- | <i>Phrynobius peraccae</i> |
| Adults more than 25 mm SVL; outer metatarsal tubercle much smaller than inner metatarsal tubercle | ----- |
| ----- | <i>Phrynobius brunneus</i> |
| 3. Skin of venter smooth; first finger longer than second | ----- |
| ----- | <i>Eleutherodactylus w-nigrum</i> |

- Skin of venter areolate; first finger shorter than second 4
4. Tympanum concealed beneath skin 5
- Tympanum visible 7
5. Digits bearing dilated pads (Fig. 1B) .. *Eleutherodactylus thymelensis*
Digital tips narrow (bulbous) (Fig. 1A) 6
6. White stripe on lip; cranial crests evident .. *Eleutherodactylus curtipes*
Lip barred; no cranial crests *Eleutherodactylus ocreatus*
7. White or cream stripe on upper lip *Eleutherodactylus buckleyi*
No cream stripe on lip 8
8. Digital pads narrow (Fig. 1A) 9
Digital pads dilated (Fig. 1B) 11
9. Vomerine teeth present on elevated odontophores 10
Vomerine teeth usually absent, no odontophore *Eleutherodactylus myersi*
10. Upper eyelid bearing several conical warts *Eleutherodactylus leoni*
- Upper eyelid smooth to shagreened *Eleutherodactylus trepidotus*
11. Canthus rostralis sharp, strongly concave (Fig. 2) *Eleutherodactylus chloronotus*
Canthus rostralis round to sharp, straight 12
12. Skin of back and flanks coarsely areolate *Eleutherodactylus orcesi*
Skin of back and flanks smooth or shagreened with or without scattered warts 13
13. Distinct tubercle on heel; males lack vocal slits *Eleutherodactylus supernatis*
Heel lacking distinct tubercle; males with vocal slits and external vocal sac 14
14. Posterior surfaces of thighs brown with or without cream reticulation; no tubercles on upper eyelid *Eleutherodactylus unistrigatus*
Posterior surfaces of thighs colorless in preservative (vermilion in life); low tubercles on upper eyelid *Eleutherodactylus modipeplus*

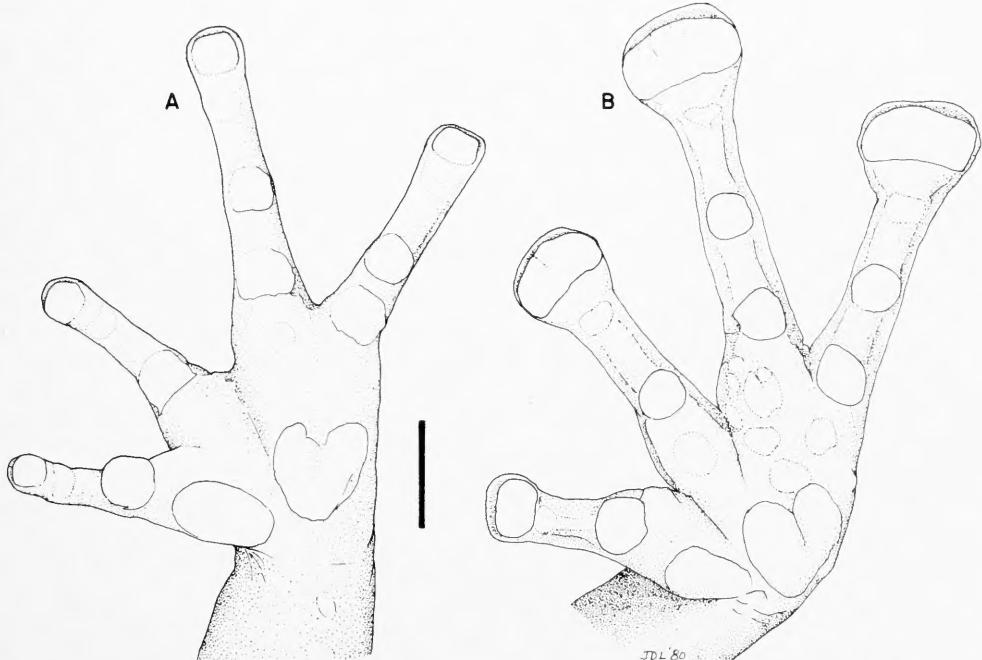


FIG. 1. Hands of (A) *Eleutherodactylus curtipes*, 10 km SW Mocha, and (B) *E. sp.*, KU 169030.
Scale equals 2 mm.



FIG. 2. Dorsal and lateral views of *Eleutherodactylus* sp. (KU 169030), scale equals 5 mm.

ACCOUNTS OF SPECIES

In the following accounts I attempt to provide comparable statements in the diagnoses and descriptions. The diagnoses consist of 14 numbered statements (or sets of statements) concerning the important characteristics of eleutherodactyline frogs followed by a phenetic diagnosis where I distinguish the taxon from those species it most nearly resembles. Measurements and proportions are given for each sex when the means differ significantly ($p < 0.05$); otherwise these data are combined.

Descriptions are not provided for *E. myersi*, *E. orcesi*, or *E. thymelensis*; the original descriptions remain adequate (Goin and Cochran, 1963; Lynch 1972b).

Eleutherodactylus buckleyi (Boulenger) Fig. 3A-B

Hylodes buckleyi Boulenger, 1882:217 (syntypes, BM 78.1.25.40-44, collected at Intac, Provincia Imbabura, Ecuador, by Mr. Buckley; BM 78.1.25.40, an adult female, is here designated the lectotype).

Diagnosis.—(1) skin of dorsum bearing low, flat warts, that of venter areolate; dorsolateral folds indistinct; (2) tympanum prominent, its length $\frac{1}{3}$ - $\frac{1}{2}$ eye length; (3) snout subacuminate in dorsal view, round in lateral profile; canthus

rostralis sharp; (4) upper eyelid narrower than IOD, lacking pungent tubercles; cranial crests present; (5) vomerine odontophores oblique in small individuals, triangular in outline in large females; (6) males lacking vocal slits and vocal sac; males bearing non-spinous nuptial pad; (7) first finger shorter than second; fingers bearing broad discs on narrow, truncate pads; (8) fingers bearing lateral keels; (9) ulnar tubercles lacking; (10) heel, outer edge of tarsus lack tubercles; tubercle on inner edge of tarsus; (11) two metatarsal tubercles, inner oval, 3-4 times size of round outer; supernumerary plantar tubercles lacking, or few and indistinct; (12) toes bearing narrow lateral fringes, no web; toe pads small, as large as those of fingers; (13) brown above with darker blotches; labial stripe white to cream; venter white to gray, spotted or reticulated with brown or not; posterior surfaces of thighs dark brown with cream spots; (14) adults moderate-sized, males 24.5-28.7 ($\bar{x} = 30.0 \pm 1.3$) mm, females 37.1-48.8 mm SVL.

Eleutherodactylus buckleyi differs from *E. curtipes* in having exposed tympana, subacuminate rather than rounded snout, less distinct dorsolateral folds,

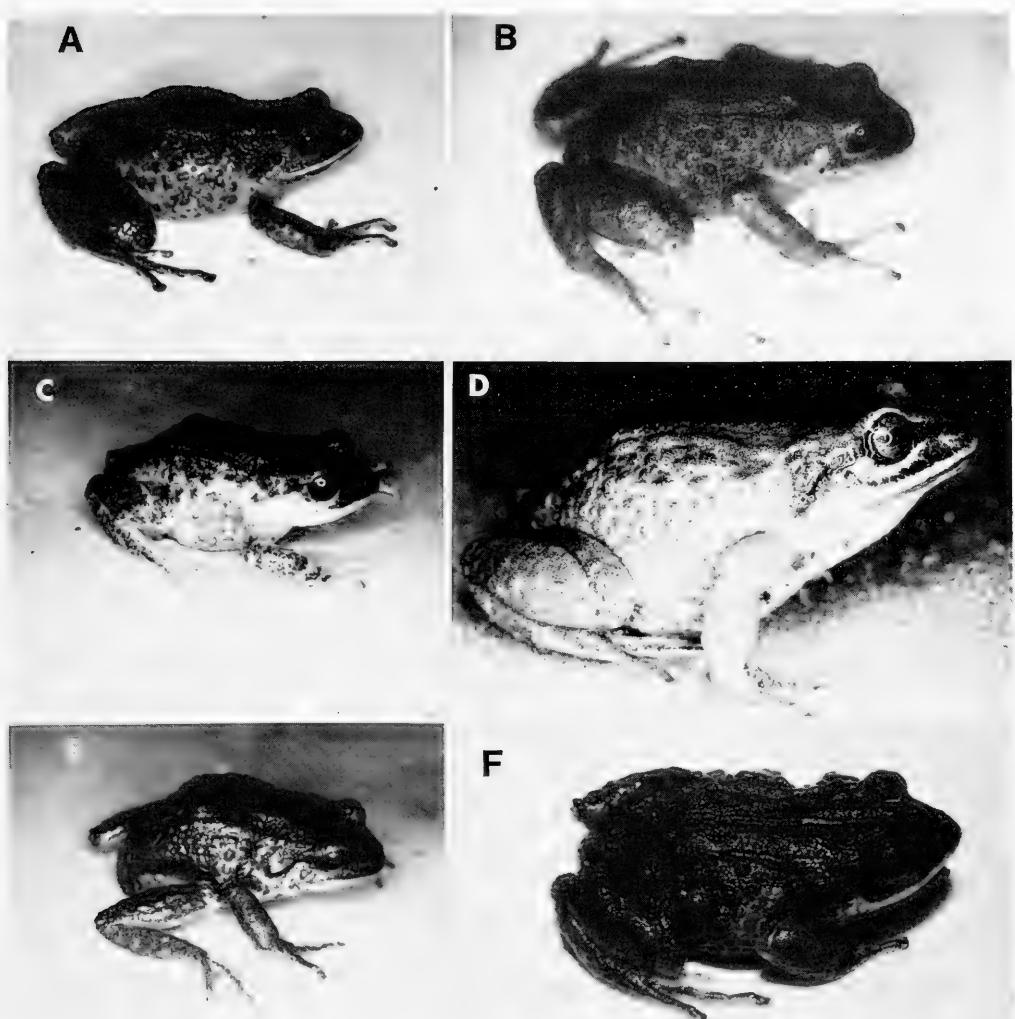


FIG. 3. (A) *Eleutherodactylus buckleyi*, KU 177225, 43.1 mm SVL; (B) *E. buckleyi*, KU 167945, 45.1 mm SVL; (C) *E. curtipes*, KU 130596, 35.2 mm SVL; (D) *E. curtipes*, Laguna de Papallacta, not preserved; (E) *E. curtipes*, KU 130597, 35.0 mm SVL; (F) *E. curtipes*, AMNH 104719, 32 mm SVL.

larger digital pads, and in greater size where the two are sympatric. The venter of *E. buckleyi* bears dark brown or black spots or reticulation whereas in sympatric populations of *E. curtipes* the venter is cream without dark markings. *Eleutherodactylus buckleyi* also resembles *E. devillei* (Boulenger) and *E. vertebralis* (Boulenger), species found in high cloud forests on the Amazonian and Pacific Andean versants of northern Ecuador. Both differ from *E. buckleyi*

in having distinct dorsolateral folds, longer hind legs, and in coloration.

Description.—Head narrower than body, wider than long; snout subacuminate in dorsal view, rounded in lateral profile; snout moderately short; canthus rostralis moderately sharp, straight; loreal region weakly concave, sloping to lips; lips not flared; interorbital space broader than upper eyelid; cranial crests heavy; upper eyelid lacking tubercles; supratympanic fold obscure, concealing

upper edge of tympanum; tympanum moderately to quite distinct, round to slightly higher than long, separated from eye by 1½ times tympanic length; choanae small, round, not concealed by palatal shelf of maxillary arch; vomerine odontophores median and posterior to choanae, generally oblique in males and juvenile females, becoming triangular in outline in adult females; odontophores bearing row of 3-5 teeth along posterior edge, separated by distance equal to choanal width; males lack vocal slits and vocal sac.

Skin of dorsum bearing low, flat warts (most evident on posterior back and flanks); dorsolateral folds not prominent; anal opening not extended in sheath; venter coarsely areolate; discoidal folds prominent; ulnar tubercles not evident; palmar tubercle bifid, larger than oval thenar tubercle; supernumerary palmar tubercles low, flat; subarticular tubercles round, nonconical; fingers lacking distinct fringes but bearing keel-like lateral ridges; all digits bearing discs (broader than long) on narrow pads; disc on thumb not distinct; first finger shorter than second.

No tubercles on knee, heel, or outer edge of tarsus; indistinct tubercle on inner edge of tarsus; inner metatarsal tubercle oval, its length twice its width, non-compressed, 3-4 times size of round, non-conical outer; few or no supernumerary plantar tubercles; subarticular tubercles round to longer than wide; toes bearing narrow lateral fringes; all toes bearing discs (broader than long) on narrow pads; hind limbs short, heel of adpressed leg reaches eye.

Brown above with indefinite darker blotching; lip stripe white to cream; venter white to pale gray, spotted or reticulated with brown or not; throat usually not spotted or reticulated in males; posterior flank, groin, anterior and posterior surfaces of thigh, concealed shank dark brown with cream spots. The testes are white in all males except those from the páramos de las Hermosas and Puracé in Deptos. Valle

and Cauca in Colombia (those frogs have black testes).

In life *E. buckleyi* is gray-tan to yellow-brown through darker browns to reddish brown or black. The dorsum is flecked with black. The toe tops are black. The pale areas on the flanks, groin, and hidden limb surfaces are creamy yellow (rarely off-white). The venter is dirty cream with brown spots or marbling (to nearly uniform black). The iris is dark chocolate-brown with a reddish cast (or copper-bronze with black reticulation and a brown horizontal streak).

Variation.—Males are smaller than females and have longer hind limbs. Specimens from the páramos de Puracé (Departamento Cauca) have larger tympana than specimens from the Nudo de Pasto and Ecuador and also have broader heads (Tables 1 and 2). The Cauca specimens are also distinctive in having darker venters than do more southern examples (Table 3).

Remarks.—Only 3 of the syntypes of *buckleyi* (BM 78.1.25.40-41, 78.1.25.43) are *E. buckleyi*. BM 78.1.25.42 is an adult female (32.3 mm SVL) *E. unistrigatus* exhibiting the striped phenotype of that species (see account of *E. unistrigatus*). The other syntype (BM 78.1.25.44) is a juvenile *Gastrotheca riobambae* (18.5 mm SVL). BM 78.1.25.40 is here designated the lectotype. Peracca (1904) reported this species from Quito. His specimens are almost certainly *E. unistrigatus*. Peracca cited Boulenger's (1882; plate 14, fig. 5) figure of *buckleyi* (based on BM 78.1-

TABLE 1. Variation in body size in male *Eleutherodactylus buckleyi*.

Locality	Range	$\bar{x} \pm 2SE$	N
P. Puracé	24.5-38.7	33.1 ± 1.7	23
La Cocha	27.4-32.5	30.2	3
Santa Barbara	25.5-37.0	30.8 ± 2.5	8
13 km SE Tulcán	25.6-34.2	29.0 ± 1.9	11
P. Angél	23.8-34.4	30.4 ± 2.8	8
Intag	27.8-34.2	31.3 ± 1.4	8

TABLE 2. Variation in proportions in *Eleutherodactylus buckleyi*. (First line, range; second line, mean \pm 2 standard errors)

Locality		(N)	Shank/ SVL	HW/ SVL	Upper eyelid/ IOD	Tympanum/ Eye
Puracé	♂	22	43.3-48.6 46.1 ± 0.6	38.7-42.4 40.3 ± 0.4	58.9-83.0 72.5 ± 3.4	38.1-55.6 48.2 ± 1.7
	♀	4	43.7-46.4 44.8	38.7-41.4	63.7-90.3 78.1	40.6-49.5 46.8
P. Angél	♂	7	41.0-46.0 43.5 \pm 1.0	36.8-40.1 38.8 \pm 1.0	69.6-100.0 78.6 \pm 7.4	32.9-40.9 35.8 \pm 1.8
	♀	4	35.8-41.7 39.0	35.5-39.1 37.0	80.0-100.0 88.5	31.1-39.0 33.5
Intag	♂	7	38.5-46.8 43.3 \pm 2.4	35.1-39.2 37.6 \pm 0.8	60.5-90.1 71.6 \pm 6.6	30.0-42.1 32.5 \pm 3.2
	♀	5	42.2-46.2 44.6	37.2-38.9 37.9	60.5-85.1 68.4	30.0-39.3 34.8

TABLE 3. Belly pigmentation (see Fig. 6) in *Eleutherodactylus buckleyi*

Locality	N	Range	$\bar{x} \pm 2SE$
P. Puracé	28	1-6	4.75 \pm 0.83
P. Angél	9	1-6	3.56 \pm 0.95
Intag	24	0-7	3.02 \pm 0.93

25.42) as identical with a pattern exhibited in his samples.

The specimens from Departamentos Cauca and Valle (Colombia) differ from specimens from more southern localities in having darker venters, black pigment on the testes, and larger tympana. Nevertheless, I consider them conspecific with material from the Nudo de Pasto.

Some frogs from the eastern face of the Llananati mountains, although superficially resembling *E. buckleyi* in size, skin texture, coloration, digital pad size, and in having cranial crests, appear to represent a new species, description of which is deferred pending acquisition of additional material. Involved are the following specimens: CAS-SU 13190, 17429-37, "El Golpe," 3000 m; CAS-SU 17439-41, Paracayacu, 2700 m; CAS-SU 17443, 17446, near Río Jorge, 3000 m; CAS-SU 10390, 10392-99, at Río San Jose, 10000 feet: all Ecuador, Prov. Napo, east face of Llananati Mts. The sample consists mostly of juveniles although CAS-SU 17437 is an adult female (42.2 mm SLV). The undescribed form,

unlike *E. buckleyi*, has the tympana concealed. The digital pads in the Llananati form are larger than those seen in the allied *E. cryophilus* and *E. curtipes*.

Distribution.—Cordillera Central of Colombia (ca. 3°30' N) south to the Nudo de Pasto; Cordillera Occidental in Ecuador (Cordillera de Intac); Cordillera Oriental in Ecuador south to Nevado Cayambe (Fig. 4). Known at elevations between 2400 and 3700 m, primarily above 3200 m.

Eleutherodactylus buckleyi is found in cloud forests as well as in páramo habitats.

Eleutherodactylus curtipes (Boulenger) Fig. 3C-F

Hylobates curtipes Boulenger, 1882: 218 (syn-types, BM 78.1.25.29-36 plus 3 others exchanged to Werner C. A. Bokermann, Marquis Doria, and the National Museum of Natural History, collected at Intac, Provincia Imbabura, Ecuador, by Mr. Buckley). BM 78.1.25.29 is here designated the lectotype.

Hylobates whymperi Boulenger, 1882: 218 (syn-types, BM 82.7.13.3 [registered as BM 1947.2.17.24], obtained at Cotocachi, Provincia Imbabura, Ecuador, 3963 m, by Edward Whymper, and BM 82.7.13.4-5 [registered as BM 1947.2.17.22-23], collected at Tortorillas, Provincia Chimborazo, Ecuador, 4024 m, by Edward Whymper). BM 82.7.13.4/ RR 1947.2.17.22 is here designated the lectotype. New synonym.

Hyla chimboe Fowler, 1913: 157 (holotype, ANSP 18137, obtained from mountains

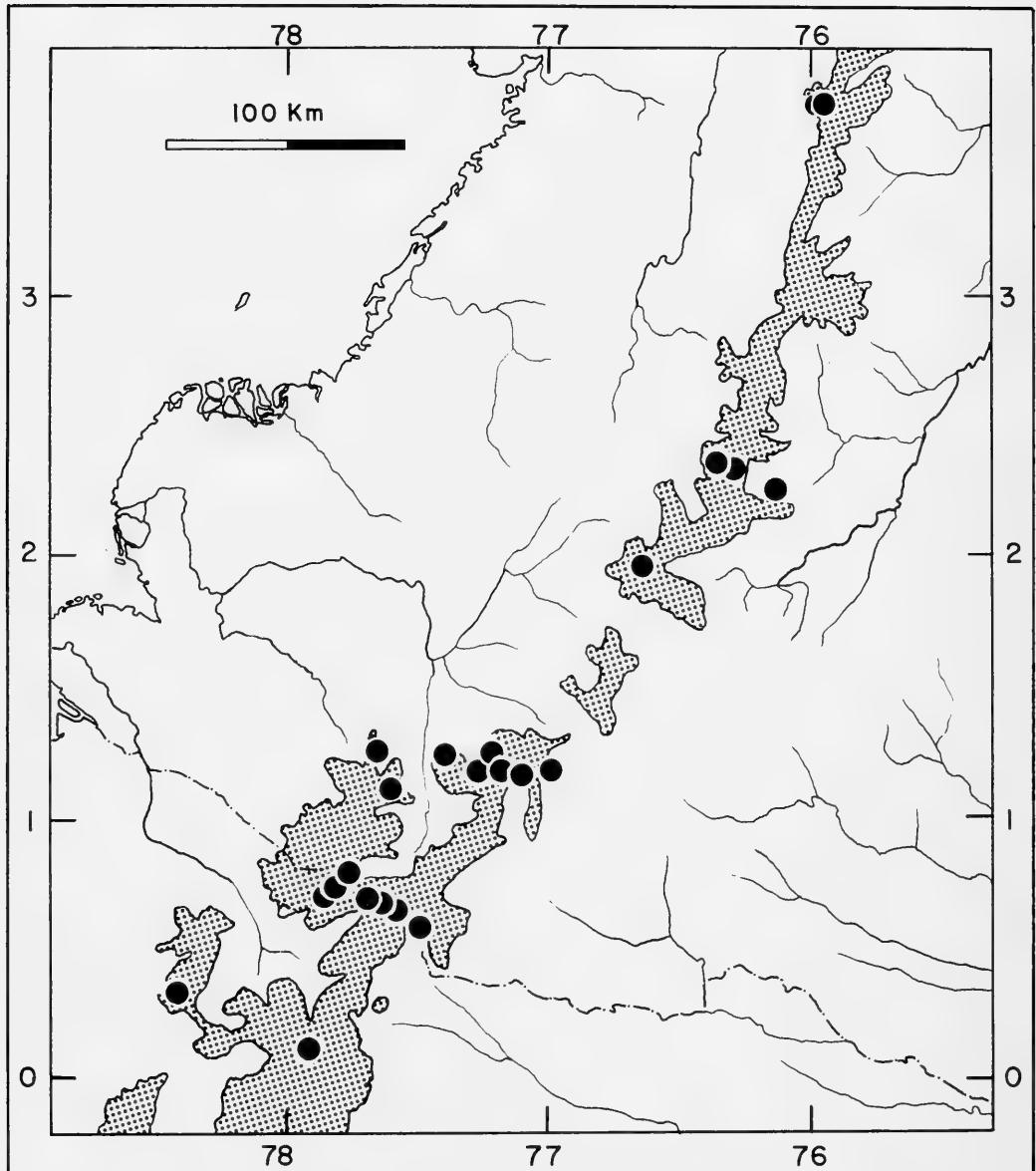


FIG. 4. Distribution of *Eleutherodactylus buckleyi*. Stippled areas lie at or above 3000 m.

above Chimbo (= San Jose del Chimbo) (probably on the Bolivar-Chimborazo frontier), Ecuador, 10000 feet, by Mr. Rhoads). New synonym.

Diagnosis.—(1) skin of dorsum bearing low, flat warts and dorsolateral folds (some paravertebral folds as well), that of venter coarsely areolate; (2) tympanum concealed beneath skin; (3) snout round to obtuse in dorsal view,

round in lateral profile; E-N < eye length; canthus rostralis obtuse; (4) upper eyelid narrower than IOD, lacking pungent tubercles; cranial crests present; (5) vomerine odontophores oblique in small individuals, triangular in outline in large females; (6) males lack vocal slits and vocal sacs; males have non-spinous nuptial pads on swollen thumbs; (7) first finger shorter than second; fin-

gers bearing discs (about as wide as long) on scarcely expanded pads; (8) fingers bearing lateral fringes; (9) ulnar tubercles normally indistinct; (10) no enlarged tubercles on heel or tarsus; inner edge of tarsus bearing thickened tubercle; (11) two metatarsal tubercles, inner oval, $1\frac{1}{2}$ to 2 times size of outer; numerous supernumerary plantar tubercles; (12) toes bearing lateral fringes, no web; toe tips as narrow as finger tips; (13) pattern and coloration variable; pale stripe on lip; dorsum usually lacking distinct markings, limbs not barred; venter cream to heavily marbled with brown (Fig. 5); (14) adults moderate-sized, males 16.0-32.5 mm SVL, females 25.9-42.9 mm SVL (see Table 4).

Eleutherodactylus curtipes differs from *E. buckleyi* in having the tympana concealed, a shorter, more rounded snout, more distinct dorsolateral folds, and in lacking distinct digital pads.

Description.—Head narrower than body, head wider than long; head width

29.9-41.8 ($\bar{x} = 37.0$, $N = 485$) percent SVL; snout rounded to obtuse in dorsal view, rounded to sloping in lateral profile, slightly overhanging lower jaw, short, E-N less than eye length; canthus rostralis obtuse (rarely moderately sharp), slightly concave; loreal region concave, sloping abruptly to lips; lips not flared except in very large females; nostrils weakly protuberant, directed dorsolaterally; interorbital distance greater than upper eyelid width; upper eyelid width 61.0-121.4 ($\bar{x} = 81.9$, $N = 291$) percent IOD in males, 60.5-108.6 ($\bar{x} = 77.4$, $N = 187$) percent in females; interorbital distance narrower in males than in females; edges of frontoparietals forming crests, crests more distinct in larger individuals; frontoparietals complete, no fontanelle; tympanum concealed beneath skin; supratympanic fold prominent, obese; tongue large, thick, not notched posteriorly, posterior one-fifth to one-third free; choanae round, completely visible on roof of mouth when viewed

TABLE 4. Variation in body size in adult *Eleutherodactylus curtipes*. Data given are: Range in mm (N) $\bar{x} \pm 2SE$. Localities are numbered as in Fig. 8.

Locality	Males	Females
1. Volcán Chiles		26.9-28.9(2)
2. 13 km SE Tulcán		26.9-31.5(3)
3. 14 km SW Tulcán	16.6-26.3(10)22.0 \pm 1.8	27.6-33.2(13)30.2 \pm 0.9
4. 20 km SW Tulcán	18.8-22.9(9)21.3 \pm 0.9	27.4-32.0(16)29.7 \pm 0.8
5. Intag		29.6-32.8(2)
6. Nudo de Mojanda	21.1-27.7(18)23.9 \pm 0.7	29.5-30.6(2)
7. Lago de Mojanda	19.2-27.5(35)23.7 \pm 0.7	25.7-36.7(20)31.4 \pm 1.0
8. V. Pichincha	21.6-30.6(12)26.3 \pm 1.6	35.3-42.9(8)40.4 \pm 1.5
9. Guamaní 3800 m	21.2-25.4(3)22.9	34.6-37.2(2)
10. Guamaní 3600 m	22.2-29.2(20)24.8 \pm 0.8	31.2-36.5(4)34.1
11. Lago Papallacta	23.7-28.4(10)26.1 \pm 0.8	33.8-35.4(4)34.5
12. vic. Papallacta	17.8-28.8(49)25.2 \pm 0.6	29.9-37.1(17)33.7 \pm 1.2
14. P. de Milín	21.8-29.6(4)24.8	30.2-40.5(10)35.9 \pm 2.2
15. P. de Apaqua	21.5-28.5(13)24.7 \pm 1.2	32.6-41.4(7)36.8 \pm 2.3
16. Guilo 3500 m	17.3-27.3(29)22.9 \pm 1.0	30.8-33.4(6)32.1 \pm 0.8
17. 12 km SW Sta. Rosa	16.7-27.0(15)23.2 \pm 1.4	32.9-37.0(2)
18. 18-20 km SW Sta. Rosa	16.3-26.2(16)22.5 \pm 1.7	
19. Arenal	16.0-26.8(11)22.5 \pm 2.0	28.2-34.4(6)31.0 \pm 2.0
20. 7-10 km W Baños	20.6-32.5(26)26.6 \pm 1.0	32.4-41.8(15)37.4 \pm 1.4
21. 10 km W Cotaló	26.6-31.8(4)28.8	32.8-40.2(3)36.5
22. 10 km SW Mocha	21.2-27.8(8)24.4 \pm 1.8	31.6-34.7(9)33.5 \pm 0.8
23. Urbina	17.4-28.9(22)25.1 \pm 1.2	27.2-39.0(38)34.6 \pm 0.7
24. W San Juan	22.6-25.6(10)24.3 \pm 0.8	30.2-35.5(12)32.3 \pm 0.9
25. E Quaranda	17.0-25.2(15)23.2 \pm 1.0	30.0-39.5(12)34.0 \pm 1.6
26. SW Cajabamba	21.7-25.9(11)23.6 \pm 0.7	32.5-37.7(5)34.5
27. SE Pungalá	19.1-21.2(2)	35.1-40.1(2)

from directly above; vomerine dentigerous processes present, median and posterior to choanae, obliquely oriented, each process two to three times size of a choana, triangular in outline in larger individuals, vomerine teeth in a transverse series across posterior edge of process, 4-7 teeth/process; dentigerous processes separated by distance equal to one-half width of a choana in large specimens, separation equal to two or three times width of choana in small specimens; males lack vocal slits and sac.

Skin of dorsum bearing a pair of ill-defined dorsolateral folds (more prominent in living than preserved examples); some specimens have faint paravertebral folds as well, these are usually striped individuals (see below); center of back pustulate, bearing low, flat warts; skin of head weakly pustulate except on upper eyelids which have low, flat warts; skin of flanks with large, low, flat warts interspaced among small warts; skin of lower flanks coarsely areolate, as is skin of venter, including throat; discoidal folds prominent to obscure, ending anterior to groin; skin of face and concealed surfaces of limbs smooth, that of exposed surfaces of limbs bearing low, flat, warts; skin on knee, heel, and elbow bearing numerous small warts; ulnar surface bearing row of tubercles, vary from indistinct to prominent, coalesce into a ridge distally extending onto edge of palm and outer edge of fourth finger; all fingers bearing lateral fringes, fingers relatively slender in females, somewhat thicker in males; first finger shorter than second; subarticular tubercles round, non-conical, simple; thenar surface with few supernumerary tubercles, outer palmar tubercle largely fused with median (= bifid palmar tubercle), inner palmar tubercle (= thenar) largest; all fingers bear apical pads with circumferential grooves; pads of third and fourth fingers wider than long, truncate, not expanded; pads of inner two fingers more rounded and smaller than those of outer fingers.

Tarsus bearing row of poorly defined tubercles along outer edge which coa-

lesce distally and continue as a fold along sole and outer edge of fifth toe; all toes fringed, fringes coalesce as basal web; inner edge of tarsus bearing thick inner tarsal tubercle lying just proximal to inner metatarsal tubercle; two metatarsal tubercles, inner larger, oval, not compressed, outer round, low; outer metatarsal tubercle is one-half to two-thirds size of inner in large specimens, in small specimens the outer is as much as four-fifths size of inner; subarticular tubercles of toes smaller than those of fingers, round, non-conical, simple; no supernumerary tubercles on toes; plantar supernumerary tubercles numerous, low, flattened; shank 34.0-45.8 ($\bar{x} = 39.2$, $N = 305$) percent SVL in males, 31.9-47.0 ($\bar{x} = 39.0$, $N = 206$) in females.

Males have large testes which are usually darkly pigmented with brown or black. The pigmentation was not found in 5.8 percent of the males examined, 17.6 percent had white testes with a black or brown network of pigment, and 76.6 percent had more or less uniform black or brown pigmentation on the testes. Some females, especially young females, have brown peppering on the peritoneum covering the ovaries.

The coloration of *E. curtipes* is highly variable. The ground color is usually dark gray or brown but specimens with yellow or gold ground color are relatively abundant in central Ecuador and specimens with reddish ground color occur throughout the range of the species. Green is rarely seen in the color pattern. The majority of specimens have indefinite darker mottling on the dorsum but some specimens have distinct blotches, usually brown, on the back. The limbs are very rarely barred. The face is not barred but a distinctive cream or white stripe is found at the edge of the upper lip. The axilla, groin, and concealed surfaces of the thigh and shank are usually unpigmented or faintly pigmented with brown. Occasional examples, mostly from central Ecuador, have pale red washes on the concealed surfaces. The dorsal pattern in some

specimens from most populations is striped—a combination of dark and cream stripes between the dorsolateral folds; the pattern is not polymorphic in *E. curtipes* but I will refer to the "striped pattern" and "normal pattern" in the discussion of interpopulation variation.

Variation.—As mentioned above, *E. curtipes* often exhibits a pattern of dorsal stripes. Striped individuals occur in every sample examined except one from the páramo de Apaqua ($N = 24$) and another from Urbina ($N = 71$). In each case, adjacent samples exhibit low frequencies of striped frogs (Guilo, 8 km W Apaqua, 13%, $N = 46$; 10 km SW Mocha, 12%, $N = 30$). Elsewhere (Table 5), striped frogs occur at frequencies between 3.9% and 69.5% but with no suggestion of a geographic pattern (Fig. 5, 6). In addition to the two cases of distinctly different frequencies in adjacent populations cited above, the two sites on the Nudo de Mojanda differ appreciably in stripe frequencies (3.9 vs 33.8%) and the two sites on the southern flank of Ne-

vado Chimborazo are markedly different (34.0 vs 69.5%) in spite of less than 10 km separations.

Eleutherodactylus curtipes also varies considerably in the extent of dark pigment on the venter (Table 5). Variation is continuous from completely cream or white venters to entirely black venters. To assess populational variation in this attribute, I coded a series of individuals for increasing degree of pigmentation (Fig. 6) and scored specimens to the best fit with the graded series. Ventral pigmentation varies geographically in that the most northern samples consist of frogs with little or no dark pigment on the venter, whereas southern samples are made up of frogs with more dense pigmentation of the venter (Fig. 5). Adjacent populations do not exhibit pronounced differences (in contrast to the case in dorsal striping). The populations with the darkest venters are found on Volcán Pichincha and SW of the Riobamba *hoya*.

Eleutherodactylus curtipes exhibits

TABLE 5. Pattern variation in *Eleutherodactylus curtipes* (see Fig. 6 for belly pattern code). Localities arranged from N to S (see Fig. 8).

Locality	% striped	Range	Belly Pattern	N
			$\bar{x} \pm 2SE$	
1. Volcán Chiles	0.0	0-1	0.50	2
3. 14 km SW Tulcán	56.5	0-4	0.52±0.43	23
4. 20 km SW Tulcán	33.3	0-3	0.22±0.24	27
5. Intag	0.0	0-1	0.50	2
6. Nudo Mojanda	3.9	0-6	2.31±0.57	26
7. Lago Mojanda	33.8	0-7	2.54±0.49	77
8. V. Pichincha	23.1	1-8	5.18±0.69	39
9-10. Paso Guamaní	47.7	0-8	2.70±0.67	43
11. Lago Papallacta	57.9	0-8	3.24±1.24	19
N slope V. Cotopaxi	55.5	1-8	4.06±1.47	9
13. Nudo Tiopullo	24.4	0-7	2.11±0.48	78
14. Páramo de Milín	30.0	0-8	2.15±0.83	34
15. Páramo de Apagua	0.0	0-6	2.79±0.78	24
16. Guilo 3500 m	13.0	0-8	3.72±0.56	46
17. 12 km SW Sta. Rosa	40.0	0-7	2.84±0.9	25
18. 15-18 km SW Sta. Rosa	38.5	0-6	2.45±0.8	22
19. Arenal	41.7	1-7	3.96±0.8	24
21. 10 km W Cotaló	14.3	0-7	2.54±1.9	7
22. 10 km S Mocha	12.0	1-6	2.42±0.65	30
23. Urbina	0.0	0-6	1.80±0.38	71
24. W. San Juan	69.5	0-9	3.48±0.7	59
25. E Guaranda	34.0	0-7	3.86±0.8	29
26. SW Cajabamba	16.7	2-9	5.90±0.8	23
27. SE Pungalá	25.0	1-6	3.25	4

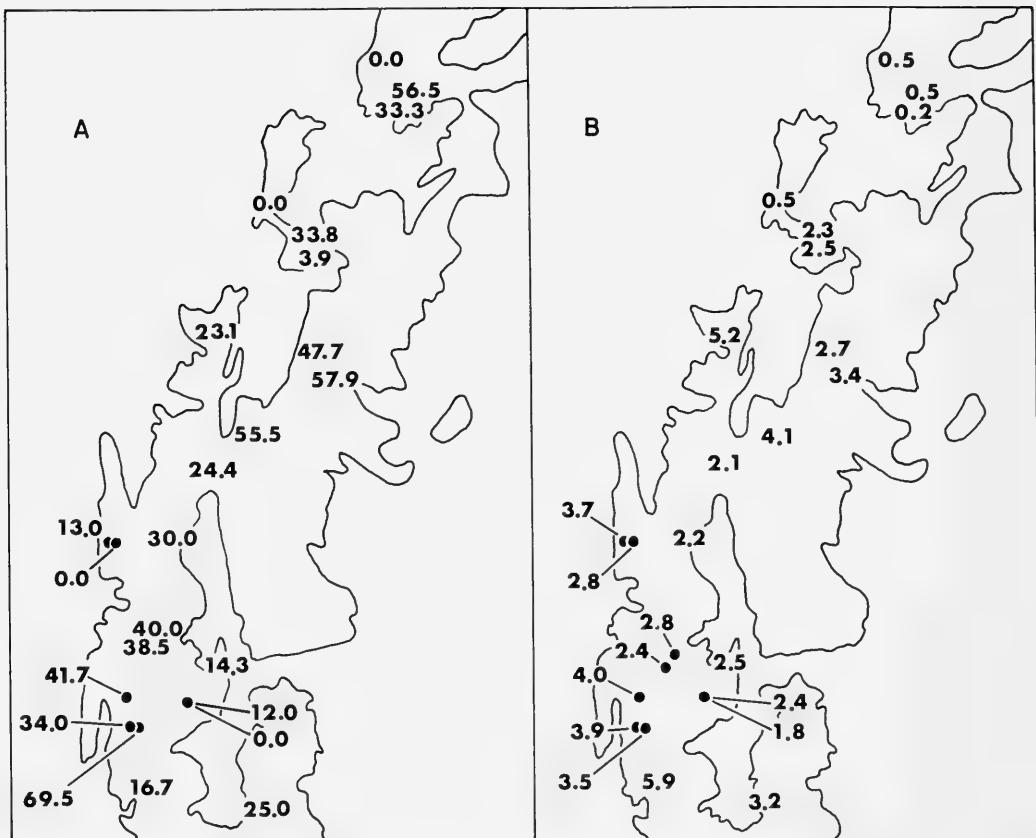


FIG. 5. Geographic variation of *Eleutherodactylus curtipes* in (A) frequency of dorsal striping and (B) ventral pigmentation. 3000 meter contour is outlined for geographic reference.

considerable variation in body size (Table 4). The smallest frogs are found in the most northern samples although small frogs also occur on the NW slopes of Nevado Chimborazo. The largest frogs are found on ridges west of the junction of the Río Chambo and Río Patate in Central Ecuador and on Volcán Pichincha. The broad overlap in sizes of adult males and adult females (24.5% of total size range), indicated in the diagnosis, is a product of marked interpopulational variation in body sizes. In only two populations (Laguna de Mojanda and W of Baños) is there actual overlap (8.0% and 0.5% respectively).

Eleutherodactylus curtipes is a short-legged frog. Except for the northernmost populations (in which legs are quite short), leg length decreases from

north to south (Table 6). The cline from the Desierto de Palmira north to the Nudo de Mojanda breaks sharply in *E. curtipes* but the sympatric *E. buckleyi* has long legs as might have been predicted for the northern *curtipes* populations. Head width does not exhibit so marked a cline but nonetheless decreases slightly from north to south (Table 6). Eyelid width relative to IOD exhibits almost no variation except that males have larger eyes than females. The high variance in males of the 10 km SW Mocha population is inexplicable (Table 6).

Natural history.—*E. curtipes* is an abundant, lapidicolous frog living in the prairie-like páramos (Fig. 7) of the northern two-thirds of Andean Ecuador. Over this geographic area, the páramo

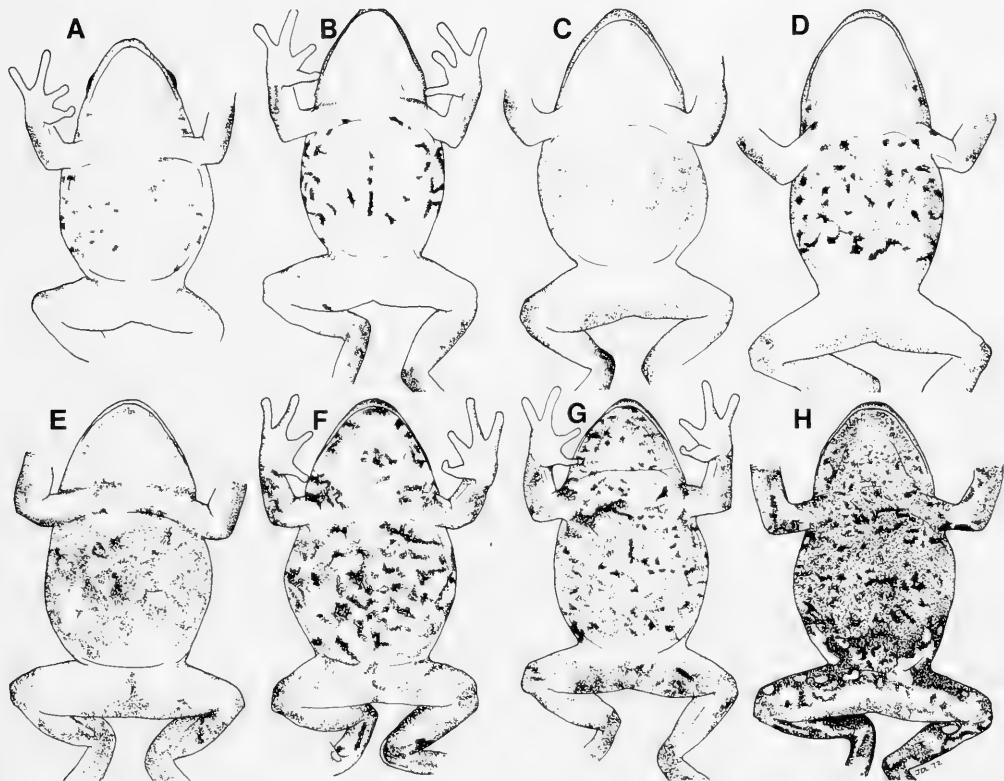


FIG. 6. Standards of ventral pigmentation in *Eleutherodactylus curtipes*. (A) KU 119604; (B) KU 119632; (C) KU 119644; (D) KU 119608; (E) KU 119656; (F) KU 119645; (G) KU 119634; (H) KU 119592. A-H are pigmentation standards 1-8. Standards 0 (completely white venters) and 9 (completely black venters) are not illustrated.

habitat occurs between 3200 and 4700 m; above 4700 m the average annual temperature is 5°C or below and the soil frequently frozen or snow-covered (Acosta-Solis, 1968). The lowest elevation at which *E. curtipes* has been found is 2750 meters (1 km W Latacunga, Provincia Cotopaxi, Ecuador). The remaining localities range from 3200 m to 4400 m. The species no doubt occurs above 4400 m but to date I have been unsuccessful in attempts to scale Nevado Cayambe or N. Chimborazo to such altitudes to search for it. At altitudes above 3200 m, *E. curtipes* is not found in the few remaining high altitude forests although other species occur there. At elevations below 3200 m in Ecuador, the predominant "forests" are *Eucalyptus* groves. In these habitats, the only

eleutherodactyline frog encountered is *E. unistriatus*. The grasslands extend below 3000 m in many areas in Ecuador but the microenvironments are perceptibly more xeric than at higher elevations and *E. curtipes* is replaced by *E. unistriatus* (Figs. 8-9). *Eleutherodactylus unistriatus* is usually parapatrically distributed relative to *E. curtipes* but I have collected them syntopically at five localities, all but one above 3200 m ("Intag", Imbabura Prov.; slopes of Volcán Pichincha, Pichincha Prov.; Nudo de Tiopullo, Cotopaxi Prov.; and 10 km W Cotaló, Tungurahua Prov.) in Ecuador. In July 1977, two *E. curtipes* were found beneath rocks beside the Río Latacunga (1 km W Latunga, 2750 m) where *E. unistriatus* is extremely common. The microhabitat was very wet;

TABLE 6. Geographic variations in proportions ($\times 1000$) of *Eleutherodactylus curtipes*. Values given are mean $\pm 2SE$ (N). Localities arranged from N to S and numbered as in Fig. 8.

Locality	Tibia/SVL		HW/SVL		eyelid/IOD	
	Males	Females	Males	Females	Males	Females
1. Volcán Chiles	364(2)	355(2)	355(2)	359(2)	954(2)	866(2)
3,4. SW Tulcán	379 \pm 013(10)	355 \pm 010(16)	351(2)	376 \pm 007(18)	818 \pm 031(18)	764 \pm 038(8)
5. Intag	427 \pm 010(8)	383 \pm 005(35)	400 \pm 008(20)	387 \pm 005(22)	756 \pm 024(35)	709 \pm 025(20)
6. Nudo Mojanda	389 \pm 005(35)	417 \pm 012(8)	352 \pm 008(12)	355 \pm 007(8)	830 \pm 035(11)	764 \pm 025(7)
7. Lago Mojanda	408 \pm 014(12)	372(2)	364(3)	343(2)	854(3)	758(2)
8. Volcán Pichincha	403(3)	410 \pm 014(11)	372 \pm 004(20)	379 \pm 010(11)	920 \pm 031(20)	840 \pm 057(11)
9. Guamani	399 \pm 006(20)	424 \pm 014(6)	354 \pm 014(10)	364 \pm 011(6)	878 \pm 036(11)	753 \pm 045(6)
10. Guamani	399 \pm 009(10)	393 \pm 011(17)	363 \pm 004(49)	366 \pm 006(17)	820 \pm 018(49)	805 \pm 036(17)
11. Lago Papallacta	390 \pm 007(49)	406(4)	367(4)	364 \pm 013(10)	871(4)	822 \pm 044(10)
13. Tiopullo	379 \pm 015(11)	388 \pm 008(7)	367 \pm 005(13)	366 \pm 008(7)	800 \pm 026(13)	669 \pm 049(7)
14. p. Milín	402 \pm 009(13)	418 \pm 011(6)	370 \pm 005(26)	369 \pm 006(6)	773 \pm 023(27)	682 \pm 023(6)
15. p. Apagua	418 \pm 007(27)	374(4)	364 \pm 006(15)	362(4)	786 \pm 025(15)	780(4)
16. Guillo	368 \pm 007(15)	362 \pm 012(16)	370 \pm 007(16)	370 \pm 0020(14)	802 \pm 020(14)	
17. SW Sta. Rosa	383 \pm 012(11)	393 \pm 016(6)	366 \pm 008(11)	378 \pm 007(13)	830 \pm 023(10)	759 \pm 050(13)
18. SW Sta. Rosa	425(4)	444(3)	366(4)	369(3)	803(4)	777(3)
19. Arenal	396 \pm 014(8)	401 \pm 012(10)	380 \pm 014(8)	373 \pm 006(10)	876 \pm 273(8)	790 \pm 036(10)
21. W Cotaló	383 \pm 009(12)	374 \pm 008(25)	394 \pm 009(12)	380 \pm 007(18)	813 \pm 045(12)	756 \pm 026(18)
22. SW Mocha	383 \pm 006(10)	388 \pm 008(20)	357 \pm 009(10)	355 \pm 004(20)	860 \pm 036(10)	814 \pm 041(20)
23. Urbina	390 \pm 010(15)	382 \pm 014(12)	383 \pm 006(15)	372 \pm 010(12)	800 \pm 049(14)	757 \pm 028(11)
24. W San Juan	377 \pm 012(11)	376 \pm 016(8)	366 \pm 010(11)	368 \pm 007(8)	880 \pm 029(11)	823 \pm 044(8)
25. E Guaranda	410(2)	380(2)	393(2)	392(2)	801(2)	701(2)
26. SW Cajabamba						
27. SE Pungalá						

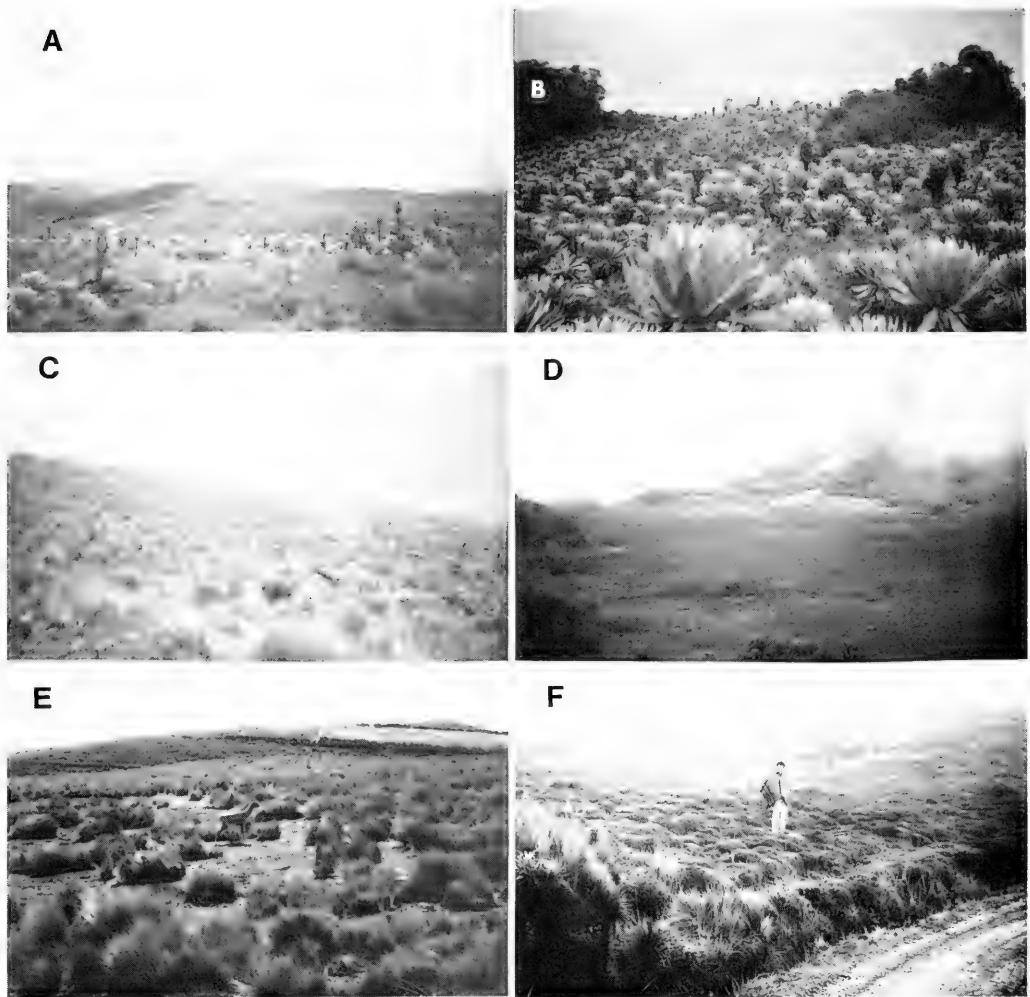


FIG. 7. Eleutherodactyline frog habitats. (A) Páramo del Angél, ca. 3800 m; (B) páramo 13 km SE Túcán, 3200 m; (C) Paso de Guamaní, ca. 4000 m; (D) Paso de Guamaní, ca. 3600 m; (E) Páramo de Apagua, 3860 m; (F) páramo 12 km SW Cajabamba, 3800 m.

when a rock was overturned, water flowed from the soil into the cavity. Additionally, some museum records suggest sympatry but without precise collecting data, altitudinal parapatry or ecological parapatry (such as *E. unistrigatus* in a *Eucalyptus* grove and 50 m away *E. curtipes* in grassland) give an illusion of sympatry. Dra. E. del Pino found both species in Machachi, Prov. Pichincha.

My analysis suggests that *E. curtipes* prefers higher, more mesic habitats (= grasslands, páramo) whereas *E. uni-*

strigatus prefers (or is forced to occupy) lower, more xeric habitats (= *Eucalyptus* groves, grassland below 3200 m). In dry páramo, such as páramo del Angél or Arenal (west falda of Nevado Chimborazo), *E. curtipes* is very locally distributed and found only along stream courses. In the páramos del Angél, most of the habitat away from the streams is occupied by *E. thymelensis*, a species smaller than *E. curtipes* but about the size of *E. unistrigatus* (Lynch, 1972b). The páramo Arenal is very much drier (Fig. 10) and all frogs occurring there

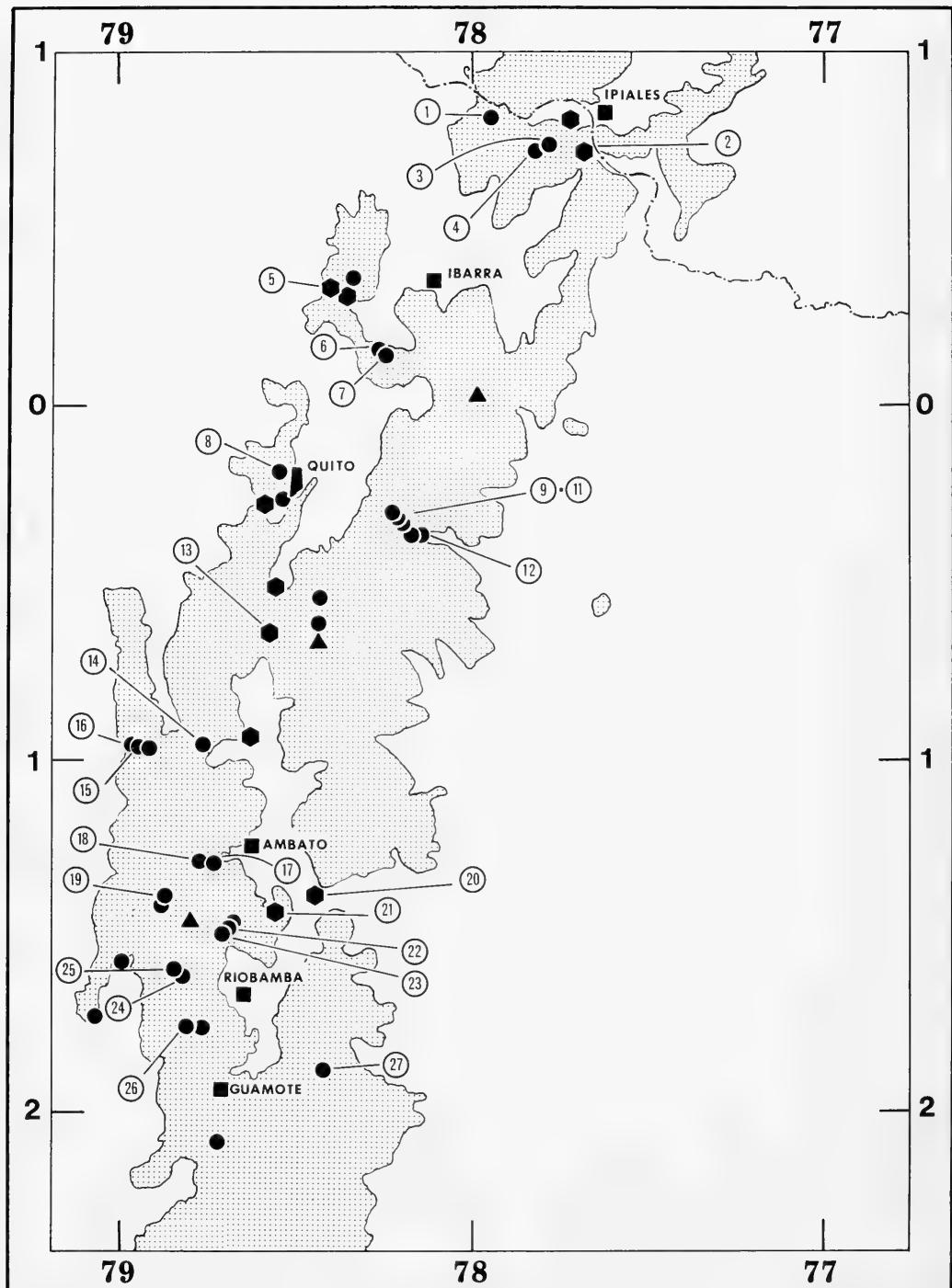


FIG. 8. Distribution of *Eleutherodactylus curtipes* (●). Numbers in circles identify localities listed in tables 4-6 and text. Six Andean towns (■) are named. Hexagons represent localities at which *E. curtipes* is sympatric with *E. unistrigatus* (Fig 9). Area above 3000 m is stippled. Major Nevados are indicated by ▲ (named on Fig. 9, facing page).

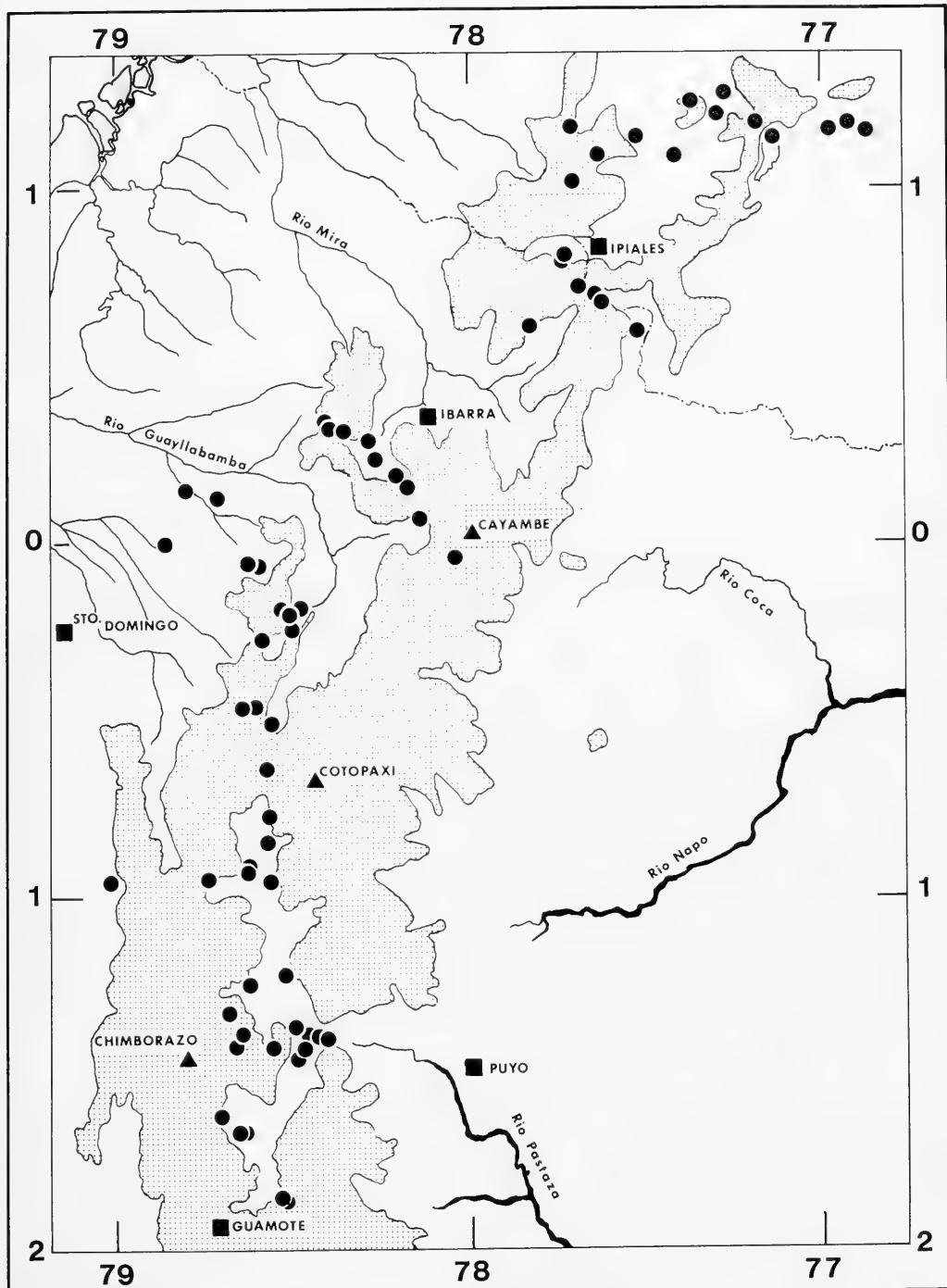


FIG. 9. Distribution of *Eleutherodactylus unistriatus* (●). Some rivers and Nevados (▲) are identified as are certain towns (■) for geographic reference. Area above 3000 m is stippled.

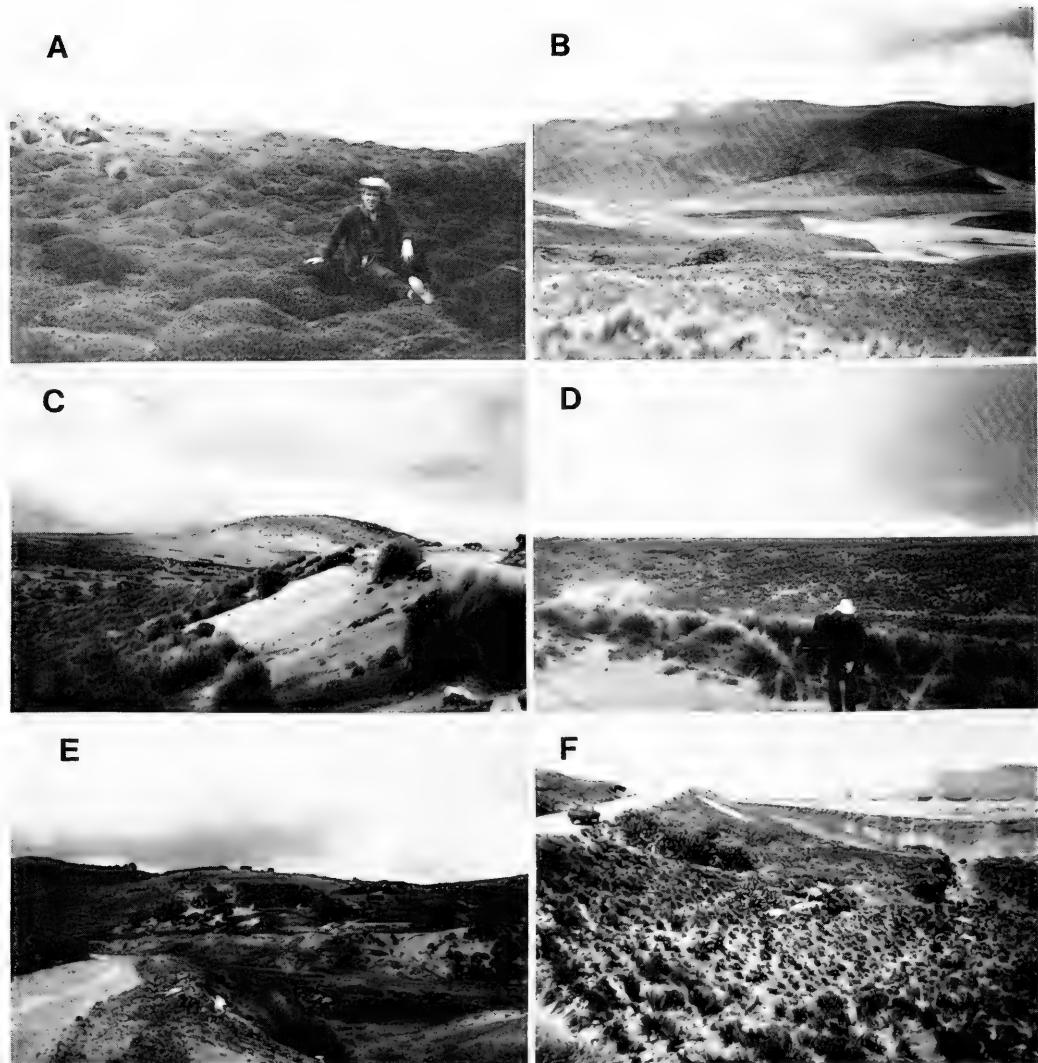


FIG. 10. Habitats of *Eleutherodactylus curtipes*. Mesic areas on east slope of N. Chimborazo, 3700 m—(A) cushion plants, (B) aspect. Xeric areas, west slope of N. Chimborazo, Arenal, 4150 m—(C-D) dry areas, (E) slightly more moist area. (F) Desierto de Palmira, N of Palmira.

are restricted to stream courses. The only *Eleutherodactylus* sympatric with *E. curtipes* at Arenal is *E. orcesi* which is about the size of *E. thymelensis* and *E. unistrigatus* (Lynch, 1972b).

In all my work in the Ecuadorian páramos I have never been certain that I heard *E. curtipes* call. *Colostethus* and *Gastrotheca* frequently are heard calling and other high altitude *Eleutherodactylus* have been traced to calling males. I have frequently heard short trilling

noises in the páramos but cannot say that the calls were not produced by insects.

I have found egg masses on only four occasions. Eggs are adherent. A mass of 19 eggs (5.2-5.4 mm diameters) was found February 23, 1968, beneath a rock at about 3600 m on the south slope of Volcán Chiles, Prov. Carchi, Ecuador (KU 118107). No frogs were beneath the rock. The eggs are early in development. The egg mass is almost certainly that of

E. curtipes although *E. thymelensis* was more abundant at the locality. On 15 July 1970, a second egg mass (KU 130466) consisting of 79 eggs (4.3-4.8 mm diameter) was dug out of an earthen bank where it was under a well-buried rock (Fig. 11). This egg mass was found at 3700 m near the frontier between Provincias Bolívar and Chimborazo (Guaranda-Riobamba road). Although *E. orcesi* probably occurs at the same locality, the number of eggs and the abundance of *E. curtipes* with ripe eggs suggest that the mass is of *E. curtipes*. These eggs are also in early stages of development.

On 14 July 1977, while marking *E. curtipes*, I found four egg masses between stones 4.7 km W Papallacta, Prov. Napo, Ecuador, 3360 m. The clutches were within 2 m of one another. KU 180286 consists of 38 eggs (diameters ca. 3.2 mm) and KU 180287 of 17 eggs (diameters ca. 4.6 mm). The other two clutches were parasitized by an unknown dipteran. KU 180288 consists of 37 eggs plus four or five capsules fused together; egg diameters are about 5.0 mm. KU 180289 consisted of more than 60 eggs, mostly destroyed by maggots.

On 27 July 1977, at 10 km SSW Mocha, frontier between Provincias Chimborazo and Tungurahua, 3450 m, I found a clutch of 30 eggs (diameters ca. 5.0 mm) and three jelly capsules (KU 180290) beneath a rock. A few centimeters away was an adult female *E. curtipes*. The eggs were in a cavity beneath the rock.

I have collected *E. curtipes* in January through March and June through August and detect no evidence of seasonality as judged from the ripe ovarian eggs present in the vast majority of adult females from each month. Young *E. curtipes* (under 13 mm SVL) have been collected at most localities and during all months collections were made. Thus reproduction is apparently aseasonal.

Eleutherodactylus curtipes is most readily collected along road cuts where there is an abundance of rocks (Fig. 11).

However, careful collecting, frequently induced by a scarcity of rocks and the crisp páramo climate, has revealed that the frogs occur at the bases of bunch grasses (*Festuca* and *Stipa*) as well as in fissures in the soil (Fig. 11). When many rocks are present, *E. curtipes* may be very abundant. For example, on 7 August 1970 I caught 80 *E. curtipes* in 30 minutes.

Lynch (1969, 1970) demonstrated that collecting habits can result in biased sex ratios in collections, so care was taken to collect in diverse sites within a locality. The combined localities yield the ratio of 263 males to 169 females among the adult *E. curtipes* measured. The higher number of males may reflect a real bias in the sex ratio or may reflect my age determination technique. Females with small ovarian eggs and thin, straight oviducts were classed as immature. Their inclusion in the female count results approximately in a 50:50 sex ratio.

Eleutherodactylus curtipes has been collected at many localities in the Andes of northern Ecuador. About 90 per cent of the extant specimens were collected in the past decade. At every locality where I found *E. curtipes*, the vegetation was largely grassland (páramo) with few scrubs or trees. The most illuminating case involves collections on the Nudo de Mojanda (Imbabura Prov.). Collecting in the vicinity of the Lagos near the top of the Nudo (3680 m) yielded numerous *E. curtipes* as well as *Atelopus ignescens* and a few *Gastropheca*. The specimens were taken beneath rocks and grass as well as from fissures in dirt banks. The vegetation consists of bunch grasses and scattered stands of a shrub (*Polylepis*) which reaches a height of 2.5-3.0 m. Tree-line in 1970 was about 3600 m; the predominantly grass páramo abruptly gave way to a relatively dense forest festooned with epiphytes and lianas. The trees reached heights of between 6 and 10 m. No *Eleutherodactylus* were found in the upper forest but at 3400 m several spe-

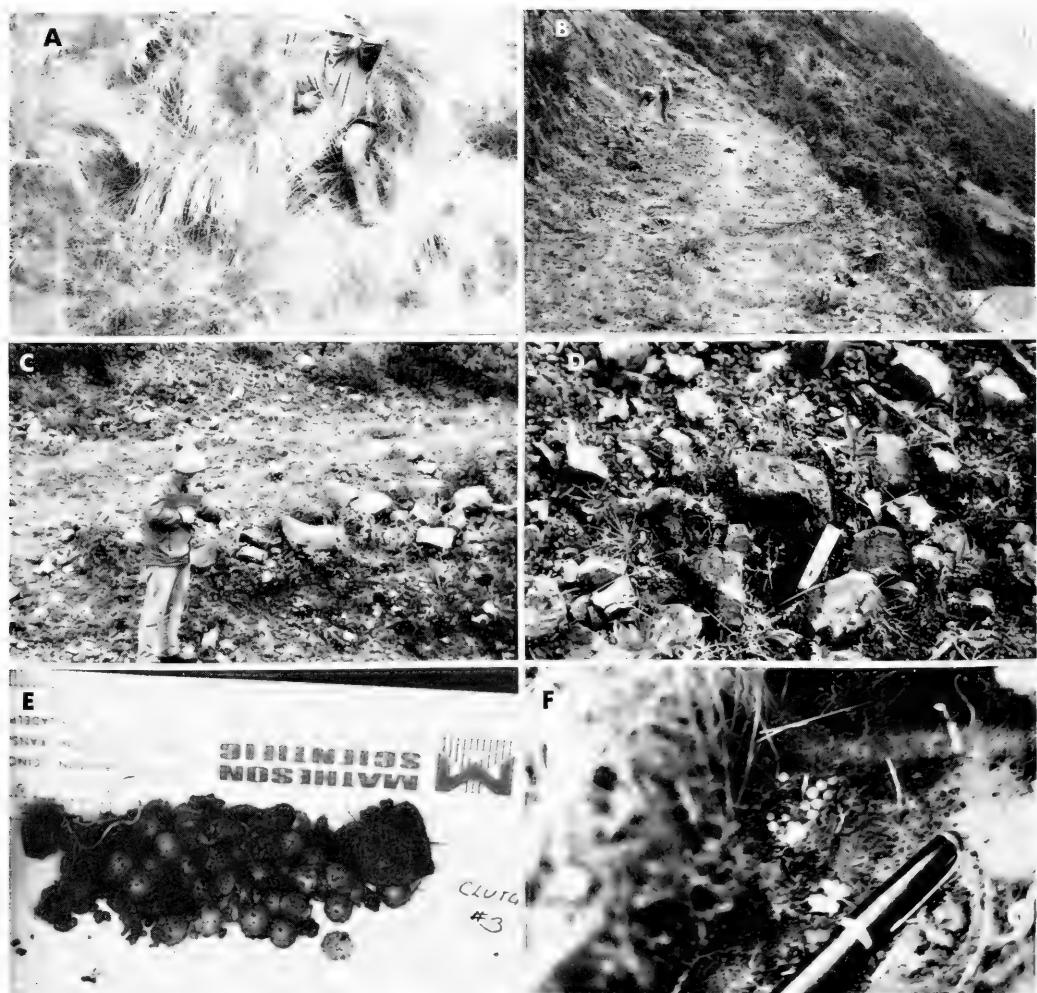


FIG. 11. *Eleutherodactylus curtipes* microhabitats: (A) bunch grass, páramo on frontier on Guaranda-Riobamba road, 3700 m; (B) rocky area, near Laguna de Papallacta, 3360 m; (C) closeup of part of B where four nests were found; (D) closeup of one nest; (E) egg mass, KU 180288; (F) egg mass, KU 130466, *in situ*, above Guaranda, 3700 m.

cies (but not *E. curtipes*) were found. At the same altitude there was a large patch (several hectares) of grassland environment. Few rocks were present but in fissures in the soil I found many specimens of *E. curtipes*. The experience of intensive collecting in distinct but adjacent communities leads me to conclude that *E. curtipes* is a páramo frog and cannot (or prefers not to) invade forested habitats. The widely introduced *Eucalyptus* forests occur in Ecuador to about 3200 m; *E. curtipes* invari-

ably occurs above the *Eucalyptus* forests and not infrequently is found in grasslands adjacent to them.

The páramos of Ecuador are probably much more widespread today than in the comparatively recent past. Before extensive deforestation, páramos evidently did not occur at elevations lower than 3600 m, if the forests on the slopes of the relatively inaccessible (until recently) Nevado Cayambe and Nudo de Mojanda are representative. If the preference for grassland habitats by *E. cur-*

tipes has not changed in response to the recent expansion of grassland habitats the distribution area of *E. curtipes* may have been significantly increased and become more continuous in the recent past through the activities of woodcutters and *carboneros*. This increase of area and development of a continuous habitat would have the effect of swamping the distinctions acquired by populations previously isolated on mountain peaks above 3600 m. Often, samples from relatively near-by localities differ appreciably in proportions and coloration (e.g., frequency of striped individuals at localities 24 and 25 or 6 and 7; mean values of belly pigmentation at localities 24 and 26); such disparities may well reflect recent isolation of populations.

Remarks.—The type-series of *Hylodes curtipes* consists of 11 specimens, of which 8 (BM 78.1.25.29-36) have been examined; 3 others were exchanged (Werner C.A. Bokermann, Marquis Doria, and USNM). The 8 are conspecific; BM 78.1.25.29, an adult female 32.8 mm SVL is here designated the lectoholotype.

The type-series of *Hylodes whymperi* includes 3 specimens; 2 (BM 82.7.13.4-5/ RR 1947.2.17.22-23) are adult males (each 25.2 mm SVL) from Tortorillas, Prov. Chimborazo, Ecuador, 4024 m. The third syntype is a juvenile female, 25.0 mm SVL, from Cotocachi, Imbabura Prov., Ecuador, 3963 m (BM 82.7.12.3/ RR 1947.2.17.24). BM 82.7.-13.4/ RR 1947.2.17.22 is here designated the lectoholotype. Boulenger (1882) distinguished *whymperi* from *curtipes* because the tympanum is partially visible in the latter, the digital pads of the latter are smaller than those of the former, and the hind limb of the former is slightly longer than that of the latter. Additionally, Boulenger (1882: 218-19) recorded the presence of an extensive frontoparietal fontanelle in *curtipes*. The frontoparietal fontanelle is not exposed in the BMNH specimens but may be in one or more of the three specimens

exchanged to other collections. The differences in distinctness of the tympanum, digit pad size, and limb length (used by Boulenger to distinguish taxa) vary geographically in Ecuador and so long as one has small sample sizes appear distinctive. Another geographically variable feature not clearly noted by Boulenger is color of the venter. He recorded the venter of *curtipes* as immaculate and that of *whymperi* as immaculate or reticulated with brown. The *whymperi* syntype having an immaculate venter is from Cotocachi near the Cordillera de Intag in Imbabura Province. The two with spotted venters are from Tortorillas on the slopes of Nevado Chimborazo, Chimborazo Prov., Ecuador. I consider the two names synonymous and in spite of line priority select *curtipes* as the name for the species (acting as first reviser).

Hyla chimboe was named by Fowler (1913) on the basis of ANSP 18137, an adult female 36.3 mm SVL. His misidentification of the specimen as a hylid insulated the name from comparison with Andean *Eleutherodactylus*. The type is a short-legged, stocky frog of the *E. unistrigatus* group having narrow digital pads, prominent cranial crests, partially concealed tympana, and a pale stripe on the upper lips. The venter is not reticulated with brown. The visibility of the tympanum may be a result of preservatives. The tympanum lies beneath the skin, now partially transparent in the temporal region, as in the type-series of *E. curtipes*. *Hyla chimboe* is here considered a synonym of *E. curtipes*.

Distribution.—*E. curtipes* occurs at elevations between 2750 m and 4400 m but is primarily distributed above 3200 m. Specimens are known from three localities virtually on the Colombian border but no specimens are available from Colombia. In Ecuador, *E. curtipes* is found on the crests of the eastern and western cordilleras (and on the connecting *nudos*) south to the Desierto de Palmira (Fig. 8). Peracca's (1904) re-

ports of *Hylodes curtipes* from El Troje and Tulcán (Prov. Carchi) and of *H. whymperi* from Papallacta (Prov. Napo) probably represent this species. His records of *H. buckleyi* from Quito (Prov. Pichincha) and El Troje, Huaca (Prov. Carchi) probably represent *E. unistriatus* whereas those for Tambo (Prov. Cañar) probably represent *E. riveti*. Peracca's (1904) report of *H. curtipes* from Paredonas, 4042 m (Azuay Prov.) probably applies to *E. riveti*.

Eleutherodactylus modipeplus

new species

Fig. 12A

Holotype.—KU 131283, an immature female taken 1 km S of the Urbina railway station, Provincia Chimborazo, Ecuador, 3650 m, on 29 July 1970 by John D. Lynch.

Paratypes.—KU 131284-85, taken syntopically with holotype.

Diagnosis.—(1) skin of dorsum sha-

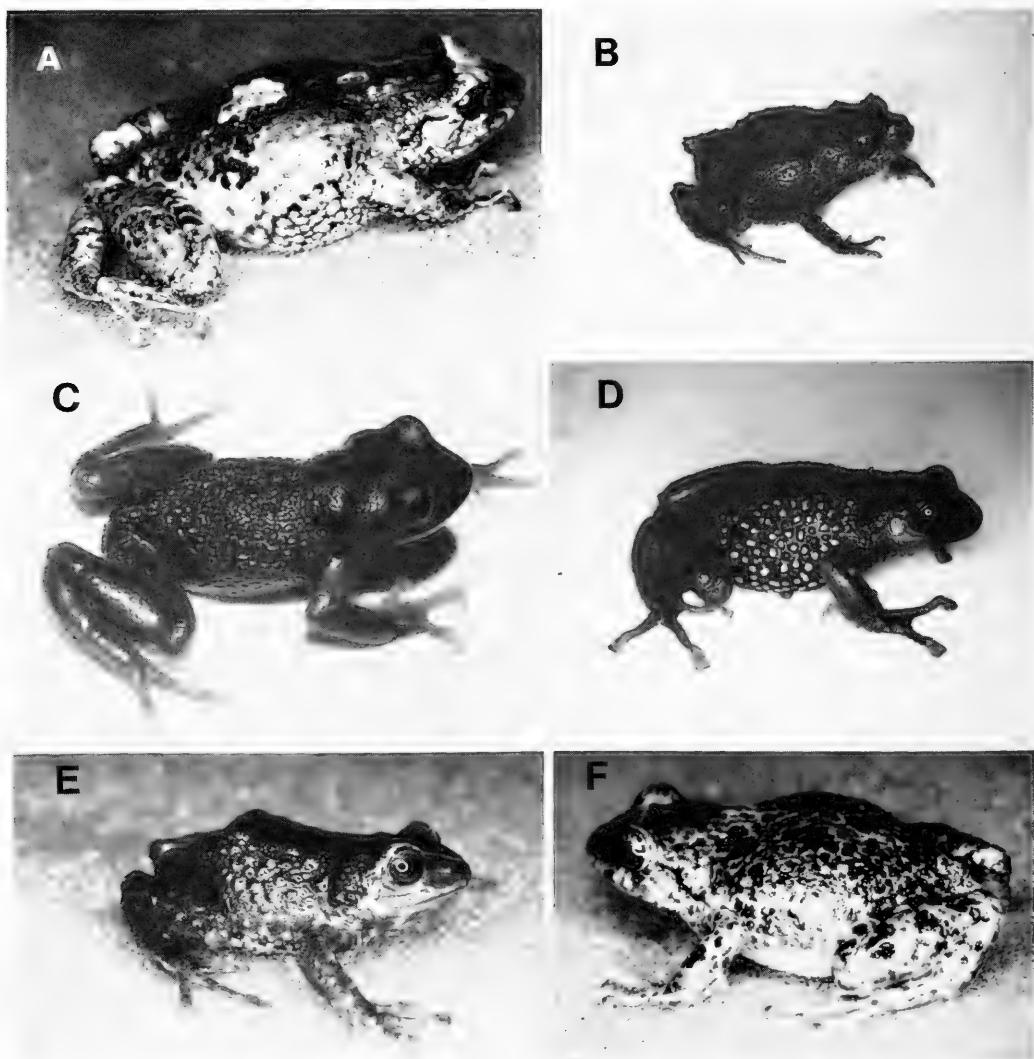


FIG. 12. Andean *Eleutherodactylus*. (A) *E. modipeplus*, KU 120021, 34.2 mm; (B) *E. myersi*, KU 168436, 18.9 mm; (C) *E. orcesi*, AMNH 104720, 32 mm SVL; (D) *E. orcesi*, KU 177814, 35.2 mm; (E) *E. thymelensis*, topotype, not preserved; (F) *E. unistriatus*, KU 119750, 28.4 mm.

greened with scattered warts, that of venter areolate; no dorsolateral folds; (2) tympanum prominent, round, its length $\frac{1}{3}$ to $\frac{1}{2}$ that of eye; (3) snout subacuminate in dorsal view, rounded in lateral profile; E-N slightly less than eye length; (4) interorbital space slightly greater than upper eyelid width; most individuals have flat interorbital region but low crests develop in large females; (5) vomerine teeth and odontophores present, odontophores slanted (teardrop-shaped), posterior and median to choanae; (6) males with vocal slits and subgular vocal sac; (7) first finger shorter than second; all digits bearing discs on dilated pads; dilation ratios I: 1.4, II: 1.7, III: 2.1, IV: 2.1; (8) fingers bearing lateral fringes; (9) ulnar tubercles poorly defined; (10) inner tarsal surface bearing one or two tubercles, outer edge of tarsus with a row of ill-defined tubercles; no prominent heel tubercles; (11) two metatarsal tubercles, outer round, conical, $\frac{1}{2}$ to $\frac{1}{3}$ size of elongate inner; numerous supernumerary plantar tubercles; (12) toes bearing lateral fringes, no basal webbing; all toes bearing discs on dilated pads, pads as large as those of fingers; (13) dorsum gray to brown with brown chevrons, interorbital bar; limb bars narrow, oblique; venter cream to nearly black; concealed limb surfaces, groin, and lower flanks pigmentless in preservative (red in life); several individuals have pale interorbital bar in front of dark bar and pale blotch edged with black in the center of the back; (14) adults small, males 24.6-28.5 mm, females 28.0-34.7 mm SVL.

Eleutherodactylus modipeplus was confused with *E. cajamarcensis* by Lynch (1969:269) who noted that *modipeplus* lacks the spotting of the venter characteristic of *cajamarcensis*. *Eleutherodactylus modipeplus* likewise lacks white spots on the black field on the posterior surfaces of the thighs. Lynch (1969) noted some partially distinguishing differences between *E. modipeplus* and *E. unistrigatus* (viz., tubercles on eyelids, low, pustular ridges on the dor-

sum, and supernumerary plantar tubercles of *E. modipeplus*).

In life, *E. modipeplus* and *E. unistrigatus* are easily separated because the former has red flash colors in the groin, anterior and posterior surfaces of the thighs, and concealed shank (cream to yellow in *E. unistrigatus*). Preserved examples of *E. unistrigatus* are subject to confusion with *E. modipeplus*. Except for the northermost populations of *E. unistrigatus*, the concealed surfaces of the thighs and groin are finely peppered with melanophores (lacking in *E. modipeplus*). The snout is more acuminate in *E. modipeplus* than in *E. unistrigatus*.

Description.—Head narrower than body, slightly wider than long; head width 36.0-39.6 ($\bar{x} = 37.3$) percent SVL; snout subacuminate in dorsal view, bluntly rounded in lateral profile; no keel on snout tip; canthus rostralis moderately sharp, concave; loreal region weakly concave, sloping abruptly to lip; lips not flared; nostrils directed dorsolaterally, not protuberant; eye length slightly greater than E-N distance, E-N 82.8-100.0 ($\bar{x} = 93.0$) percent eye length; interorbital space flat in most individuals but low lateral crests occur in large females (KU 120021, 34.2 mm SVL, and 142134, 34.7 mm SVL); no frontoparietal fontanelle; upper eyelid width 71.1-83.1 ($\bar{x} = 78.0$) percent IOD; tympanum prominent, round, its upper edge concealed by thick supratympanic fold; tympanum length 35.3-45.8 ($\bar{x} = 41.1$) percent eye length, not sexually dimorphic; choanae small, round, situated well lateral on palate, completely visible when palate is viewed from directly above; vomerine odontophores between and posterior to choanae, each twice as large as a choana; odontophores not elevated, slanted (teardrop-shaped), bearing 2-6 teeth in a slanted row, separated by distance less than choanal width; tongue large, longer than wide, weakly notched posteriorly, posterior one-third to two-fifths not adherent to floor of

mouth; males with vocal slits and sub-gular vocal sac.

Skin of dorsum shagreened with scattered low warts; enlarged warts most numerous on posterior portion of back; upper eyelid tuberculate; no dorsolateral folds; flank bearing large, flat warts; venter coarsely areolate; discoidal folds prominent.

Series of indefinite ulnar tubercles present; one bifid palmar tubercle or two palmar tubercles (median larger); larger palmar tubercle larger than oval thenar tubercle; a few low supernumerary tubercles on thenar surface; subarticular tubercles large, round, non-conical, simple; digits fringed (including outer edge of hand and fourth finger); all digits bearing discs on dilated pads, pads broader than long on all digits but pad of thumb smallest; dilation ratios I: 1.2-1.6 ($\bar{x} = 1.4$), II: 1.5-2.2 ($\bar{x} = 1.7$), III: 1.8-2.6 ($\bar{x} = 2.1$), IV: 1.7-2.4 ($\bar{x} = 2.1$); tarsus bearing one to two small tubercles along inner edge; outer edge of tarsus bearing a row of indefinite tubercles (none prominent); no enlarged tubercles on heel; hind limbs short, heel of adpressed leg extends to between posterior corner of eye and tympanum; shank 43.2-51.1 ($\bar{x} = 46.9$) percent SVL; two metatarsal tubercles, outer rounded, conical, one-fifth to one-third size of elongate (length twice width), non-compressed inner metatarsal tubercle; numerous supernumerary plantar tubercles; subarticular tubercles of toes like those of fingers; toes bearing lateral fringes, no basal webbing; toes bearing discs on dilated pads, pads broader than long, smaller than those of outer fingers.

In preservative, the ground color (all dorsal surfaces but limited to an interrupted line atop thigh) gray to gray-brown with brown chevrons and elongate spots edged with cream; some spots, especially on lower back, are spotted with black; interorbital band prominent, black or dark brown with an off-white to cream band anterior to the black band; some individuals have an off-white to

cream blotch above sacrum; the spot is irregularly edged with black; the flanks are not spotted or barred; shank and forearm bear oblique bars, slightly narrower than pale interspaces; canthal and supratympanic stripes not prominent; lips barred; venter cream with white infusion in most individuals; some have faint gray reticulation on belly; groin, anterior and posterior thigh not pigmented but the thigh may have some brown reticulation on the upper portion of the posterior surface. The individuals in the type-series have a dark-brown ground color and little pattern is evident beyond the interorbital bar and sacral spot. These individuals also have brown venters with some mottling on the throat.

In life, *E. modipeplus* is brown to reddish-brown with creamy-tan interorbital bar and sacral spot (both edged with black). The groin, axilla, concealed thigh and concealed shank are reddish-orange to blood red. The throat of males is pale yellow. The venter is dirty cream with or without gray and brown marbling. The iris is gray marbled with brown and having a medium reddish-brown horizontal streak.

Measurements of the holotype in mm.—SVL 25.7, shank 12.0, head width 9.5, upper eyelid width 2.4, IOD 3.1, tympanum length 1.2, eye length 2.8, E-N 2.7. The holotype is an immature female with straight (non-convoluted) oviducts and small cream ovarian eggs.

Etymology.—Latin, *modicus* (modest) and *peplum* (robe or tunic), in reference to the less ornate flash-colors compared with *E. cajamarcensis* (no black and white marbling).

Natural history.—All specimens of *E. modipeplus* I found were taken by day beneath rocks, clumps of dirt, or bunches of páramo grass. Gravid females have been found in June and August. Specimens captured in July 1977 (10 km SW Mocha, Prov. Tungurahua, 3700 m) and kept live in aquaria regularly called until late August when they died. The call is a sharp whistle and markedly unlike the call of *E. uni-*

strigatus. James A. Peters secured calling males on bushes 2 km S Mocha, Prov. Tungurahua, 3000 m.

The type-series was found beneath a large flat rock beside a stream. Three individuals were captured but two others jumped into the stream and escaped. Specimens collected in 1968 (10 km SW Mocha) were found beneath clumps of dirt in a dried-up vernal pond.

Eleutherodactylus unistriatus has not been taken sympatrically with *E. modipeplus* but the two surely occur together. The usual congeneric sympatrant is *E. curtipes*. The breeding season of *E. unistriatus* is from late December until February. *E. modipeplus* appears to breed during June and July but too little data are available to be conclusive. *E. modipeplus*, like *E. curtipes*, may breed all year long at higher (3200-3700 m) altitudes.

Remarks.—In my redescription of *E. cajamarcensis* (Lynch, 1969), it was distinguished from *unistriatus* in part by the "slightly smaller" digital pads of *cajamarcensis* (p. 269). That statement is in error. The dilation ratios of the hand of *cajamarcensis* are as follows: I: 1.2-1.7 ($\bar{x} = 1.4$), II: 1.6-2.0 ($\bar{x} = 1.8$), III: 1.9-2.2 ($\bar{x} = 2.1$), IV: 1.9-2.3 ($\bar{x} = 2.2$). The values for *unistriatus* are: I: 1.1-1.4 ($\bar{x} = 1.2$), II: 1.4-1.8 ($\bar{x} = 1.5$), III: 1.4-2.0 ($\bar{x} = 1.7$), IV: 1.4-1.9 ($\bar{x} = 1.7$). The dilation ratios of *modipeplus* are not appreciably different from those of *cajamarcensis*, but both have slight larger digital pads than does *E. unistriatus*.

Distribution.—Known only from the edges of the Ambato-Riobamba *hoya* (Fig. 13) in central Ecuador at elevations between 2560 and 3700 m.

Eleutherodactylus myersi (Goin and Cochran) Fig. 12B

Trachyphrynus myersi Goin and Cochran, 1963: 502 (holotype, CAS 85177, an adult female obtained "20 miles east of Pasto," Depto. Nariño, Colombia, on 1 March 1955 by E. S. Ross).

Eleutherodactylus myersi: Lynch, 1968:295.

Diagnosis.—(1) skin of dorsum pustulate, bearing paravertebral and sinuate dorsolateral ridges, that of venter areolate; no anal sheath; (2) tympanum visible, its length $\frac{2}{3}$ - $\frac{3}{4}$ eye length; (3) snout subacuminate in dorsal view, rounded in lateral profile, bearing papilla at tip; canthus rostralis sharp; (4) upper eyelid bearing numerous low tubercles, its width 51.7-79.2 ($\bar{x} = 65.9$, $N = 18$) percent IOD: no cranial crests; (5) vomerine odontophores absent, 0-2 vomerine teeth; (6) males with vocal slits, white nuptial pad on thumb, black lining of testes; (7) first finger shorter than second; fingers bearing discs and small pads; (8) feeble lateral keels on fingers; subarticular tubercles flat; (9) low ulnar tubercles present; (10) non-conical tubercles on outer edge of tarsus; short inner tarsal fold; (11) two metatarsal tubercles, inner oval, 3-4 times size of outer; numerous supernumerary plantar tubercles; (12) toes bear narrow lateral fringes; toes with narrow pads and discs; (13) brown above, black below; pale spots in groin and anterior and posterior surfaces of thighs (spots red in life); inner digits cream; (14) adults small, size geographically variable (see below), males 13.7-17.5 mm, females 17.5-23.2 mm SVL.

Eleutherodactylus myersi is most similar to *E. trepidotus* but differs in lacking vomerine odontophores and in having outer tarsal tubercles and distinct ridges on the dorsum.

Description.—Goin and Cochran (1963); Cochran and Goin (1970).

Variation.—Although known from few specimens and only nine localities, geographic variation in size is apparent. Specimens from the Pasto region are larger than those from the Páramo de Puracé: Pasto male 17.8 mm SVL, females 19.9-23.2 ($\bar{x} = 21.6 \pm 0.8$, $N = 7$) mm SVL; Puracé males 13.7-13.8 mm SVL ($N = 2$), females 17.5-20.9 ($\bar{x} = 18.8 \pm 1.2$, $N = 5$) mm SVL.

Distribution.—Known from páramos on the Nudo de Pasto and the southern end of the Cordillera Central in Co-

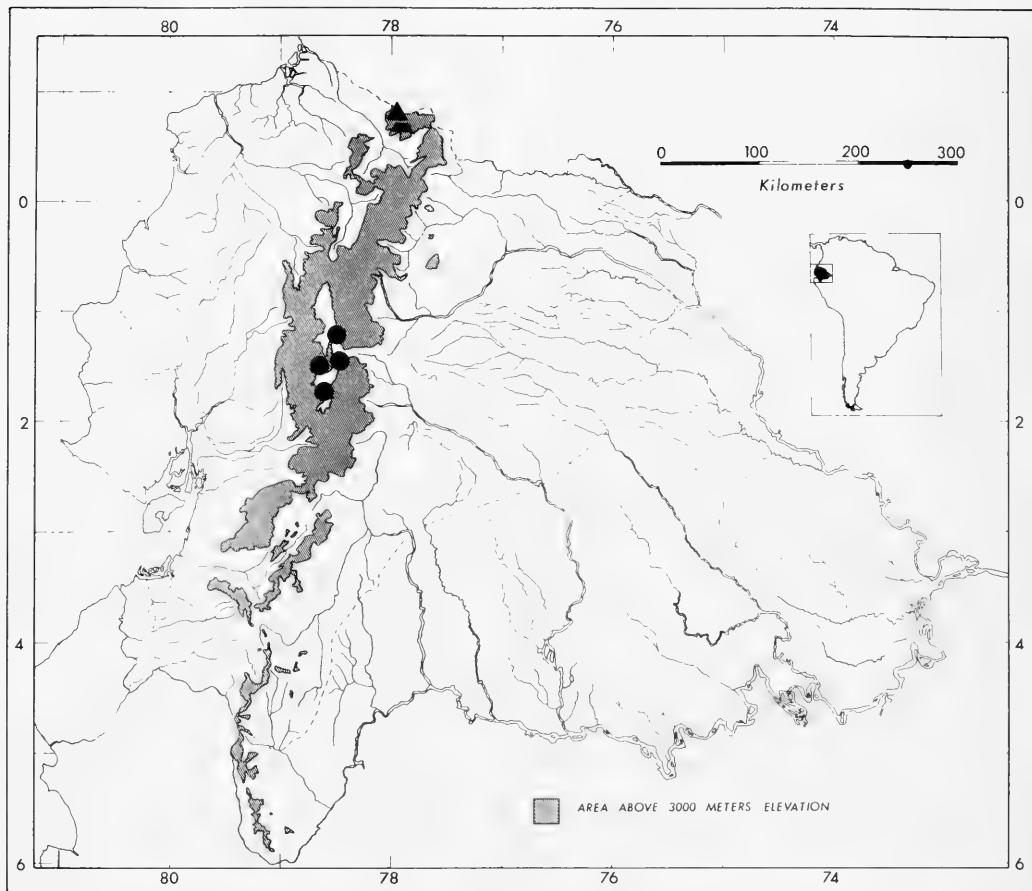


FIG. 13. Distributions of *Eleutherodactylus modipeplus* (●) and *E. ocreatus* (▲) in Ecuador.

lombia at elevations between 2900 and 3275 m.

Eleutherodactylus ocreatus new species

Eleutherodactylus myersi (part): Lynch, 1968, 295, 289-99.

Holotype.—KU 117573, an adult female collected on the west slope of Volcán Chiles, 10 km W Tufiño, Prov. Carchi, Ecuador, 3500-3800 m, on 23 February 1968 by John D. Lynch.

Paratypes.—KU 117574-81, taken with the holotype.

Diagnosis.—(1) skin of dorsum bearing low ridges, finely areolate, subconical warts on flanks; upper eyelid bearing low tubercles; (2) tympanum concealed; (3) snout round in dorsal and lateral

profiles, short; (4) interorbital space flat (no cranial crests), broader than upper eyelid; (5) vomers lacking odontophores; (6) males with short vocal slits, internal vocal sac; testes dark brown; (7) first finger shorter than second; fingers lacking pads; (8) fingers lacking lateral fringes; subarticular tubercles non-pungent; (9) ulnar tubercles not distinct; (10) no enlarged or distinctive tubercles on heel or tarsus; (11) two metatarsal tubercles, inner large, not compressed, two to three times size round, non-pungent outer; (12) toes lacking lateral fringes, webbing, pads; (13) brown to dark-brown with pale spots in axilla and groin (white with pink cast in life); venter dark brown, spotted with cream or not; (14) four males 12.4-17.2 ($\bar{x} =$

14.4) mm SVL, two adult females 19.6-20.2 mm SVL.

Eleutherodactylus ocreatus is most similar to *E. trepidotus* and *E. vidua* but differs from both in lacking vomerine odontophores. *Eleutherodactylus myersi*, with which *E. ocreatus* was previously confused by me, is readily distinguished in having small, albeit perceptible, digital pads (Fig. 14) and a larger, more obvious tympanum (Fig. 15).

Description.—Head as broad as body except in adult females (where narrower than body), wider than long; head width 34.8-37.9 ($\bar{x} = 36.6, N = 6$) percent SVL; snout rounded in dorsal and lateral views; nostrils weakly protuberant, directed dorsolaterally; snout very short, E-N 51.5-71.4 ($\bar{x} = 62.0, N = 6$) percent eye length; canthus rostralis rounded to obtuse; loreal region weakly concave,

sloping gradually to lips; lips not flared; interorbital space flat, no cranial crests; upper eyelid 79.1-93.8 ($\bar{x} = 85.1, N = 6$) percent IOD, bearing rounded, non-conical warts; tympanum concealed beneath skin; upon drying, annulus visible, its length 32.5-48.5 ($\bar{x} = 40.4, N = 5$) percent eye length, separated from eye by one annulus length; supratympanic fold not prominent; tympanic region not vertical; temporal region not swollen; postrostral tubercles not conical; choanae small, round, not concealed by palatal shelf of maxillary arch when roof of mouth is viewed from directly above; vomers lacking odontophores; tongue elongate (length 2½ times width), not notched posteriorly, posterior $\frac{1}{3}$ not adherent to floor of mouth; males with short vocal slits near angle of jaws, vocal sac internal.

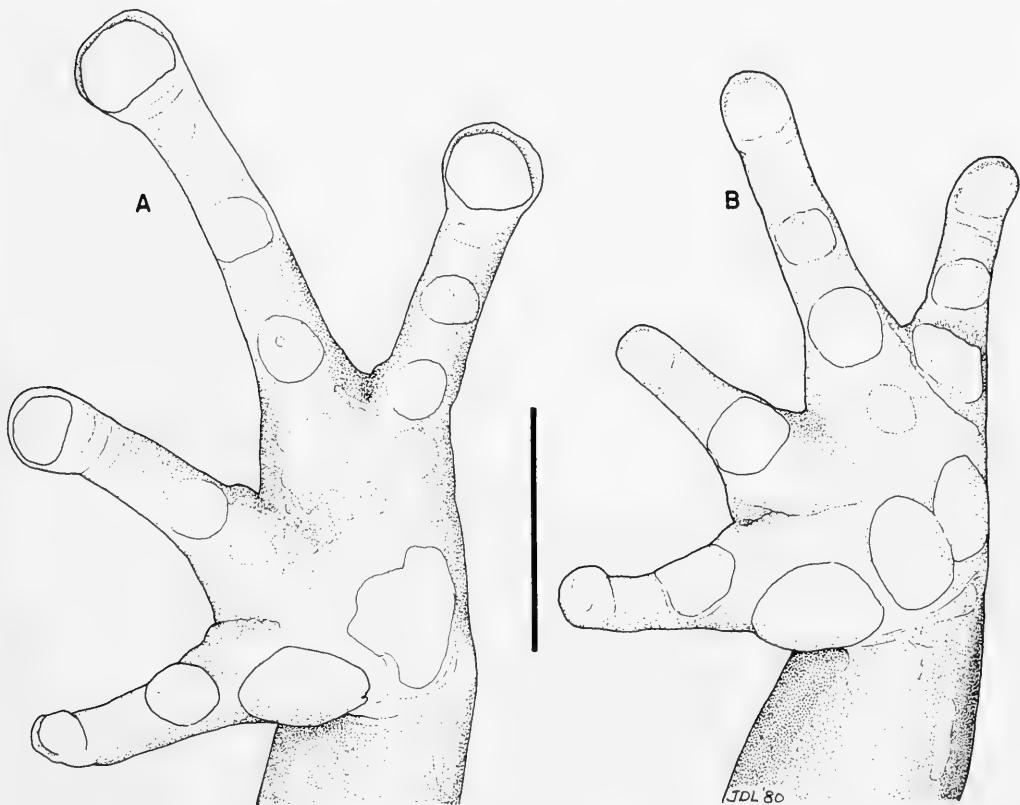


FIG. 14. Palmar views of hands of (A) *E. myersi*, AMNH 86752, and (B) *E. ocreatus*, KU 117574. Scale equals 2 mm.

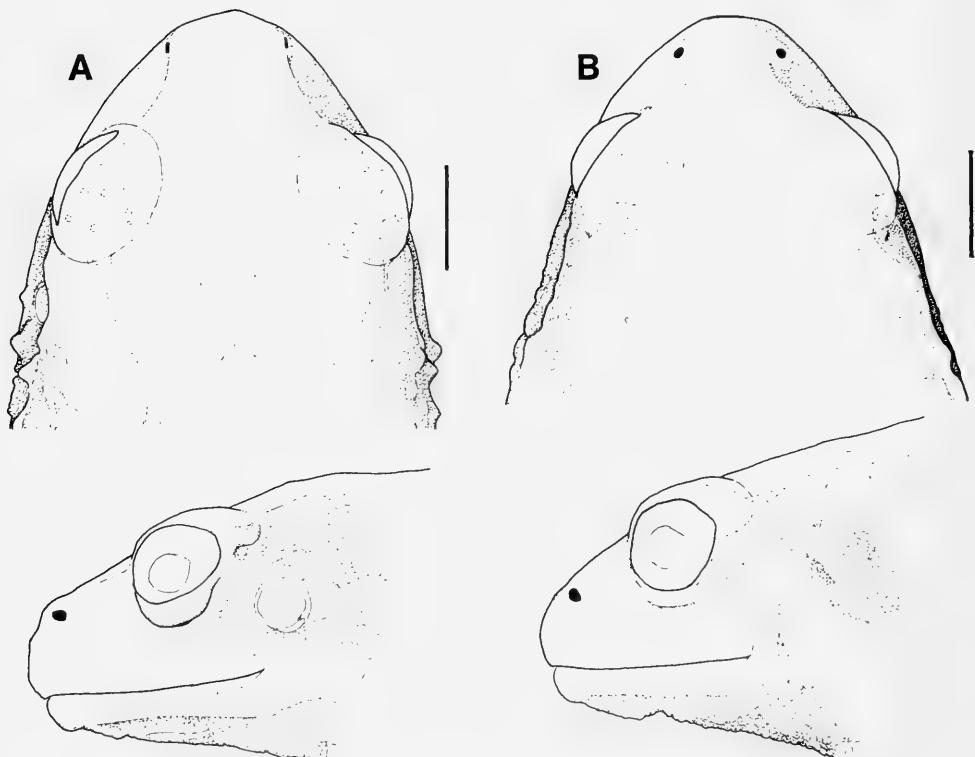


FIG. 15. Dorsal and lateral views of heads of (A) *Eleutherodactylus myersi*, AMNH 86752 and 86753 and (B) *E. ocreatus*, KU 117574. Scale equals 2 mm.

Skin of dorsum smooth anteriorly, finely areolate posteriorly and laterally, bearing low paravertebral and dorsolateral folds; skin of lower flanks coarsely areolate (warts subconical), that of venter coarsely areolate; discoidal folds prominent; anal opening not modified; no inguinal glands; limbs smooth with subconical warts; ulnar tubercles not prominent; palmar tubercle bifid, as large as oval thenar tubercle; supernumerary palmar tubercles indistinct; subarticular tubercles non-pungent, broader than long; fingers lacking fringes and pads; discs (as long as wide) on fingers III and IV; first finger shorter than second.

No tubercles clearly identifiable on heel or tarsus (tarsus is tuberculate, as is leg); inner metatarsal tubercle twice as long as wide, large, not compressed, two to two and one-half times size of round, non-pungent outer metatarsal tu-

bercle; supernumerary plantar tubercles non-pungent; subarticular tubercles non-pungent, round or weakly elongate; toes lacking fringes and pads; hind legs very short, shank 32.8-41.1 ($\bar{x} = 36.9$, $N = 6$) per cent SVL.

Above brown with diffuse darker brown mottling; dark tan interorbital bar present or not; middorsal raphe from scapula to vent present or not, if present, cream edged with reddish-brown; individuals having dorsal raphe have cream line down midline on venter and another (perpendicular) across breast; groin and axilla bearing cream spots; posterior surfaces of thighs brown with cream marbling; venter dark brown, usually spotted or marbled with cream; hands and feet, except outer edge, white, as are top of foot and tarsus and underside of shank.

In life, *E. ocreatus* was colored as follows: "Dorsum and upper flanks dark brown, in some a reddish-brown mid-

dorsal stripe or broad dorsal band (= raphe); most have pale orange spots along dorsolateral folds; flanks and venter black with white spots; posterior surface of thigh fuscous brown with pale yellow spots; the spots in axillae tend to pink; in some specimens, there is a cross on the venter, very pale pink; iris blue-gray; inner digits pink to cream" (J. D. Lynch field notes 23 February 1968).

Measurements of holotype in mm.—SVL 19.6; shank 7.2; head width 6.8; head length 6.2; upper eyelid width 1.7; IOD 2.2; tympanum length 1.05; eye length 2.2; E-N 1.45. The holotype is a gravid female with extensively convoluted oviducts.

Etymology.—Latin, *ocreatus*, meaning wearing leggings or booted, in reference to the pale hands and feet which appear clothed in gloves and socks.

Natural history.—The nine specimens were collected by day beneath rocks and clumps of dirt in non-burned areas of the páramo. The area was recently burned but some enclaves of green grass remained; presumably these areas were wetter than the burned areas. Both adult females are gravid. The thumbs of the males are swollen but do not possess nuptial pads. The testes are dark brown (presumably black in life). The ovarian linings are peppered with brown in the three juvenile females.

Remarks.—*E. ocreatus* is mostly closely related to *E. trepidotus* found at comparable or slightly lower elevations on the Amazonian versant of the Andes in northern Ecuador. The two are similar in size and proportions, morphology of the hands and feet, and in color pattern.

Eleutherodactylus ocreatus is sympatric with *E. curtipes* and *E. thymelensis*; both are larger frogs. Further collecting may show that the still larger *E. buckleyi* is sympatric with *E. ocreatus* in the Páramos del Angél.

Distribution.—Known only from the Páramos del Angél (3500-4150 m) in extreme northern Ecuador (Fig. 13).

Eleutherodactylus orcesi Lynch

Fig. 12C-D

Eleutherodactylus orcesi Lynch, 1972:142
(holotype, KU 130316, an adult female obtained 5 km SW Bolívar-Chimborazo frontier on Guaranda-Ambato road [= 24.8 km by road N Guaranda], SW slope of Nevado Chimborazo, Prov. Bolívar, Ecuador, 3800 m, on 17 July 1970 by J. D. Lynch).

Diagnosis.—(1) skin of head smooth, that of dorsum, flanks, and venter areolate; no dorsolateral folds; (2) tympanum visible, its length $\frac{1}{2}$ eye length; (3) snout short; snout round in dorsal and lateral profiles; canthus rostralis sharp; (4) IOD broader than upper eyelid; no cranial crests; no tubercles on eyelid; (5) vomerine odontophores absent; (6) males with vocal sac and slits; white nuptial pad on thumb in males; (7) first finger shorter than second; pads of outer fingers as large as tympanum; (8) fingers bear narrow lateral fringes; (9) ulnar tubercles absent; (10) no tarsal tubercles; a small heel tubercle; (11) two metatarsal tubercles, inner oval, 3-5 times size of outer; numerous supernumerary plantar tubercles; (12) toes bear lateral fringes; toe pads as large as those of fingers; (13) brown to black above with or without white warts on flanks; venter pale brown; no limb or lip markings; (14) adults small, males 23.9-29.6 ($\bar{x} = 26.5$, $N = 7$) mm, females 35.2-36.1 ($\bar{x} = 35.8$, $N = 3$) mm SVL.

Eleutherodactylus orcesi is not easily confused with other species. Its nearest relative is *E. thymelensis* which is easily distinguished in having the tympana concealed and in having vomerine teeth.

Description.—(Lynch, 1972b).

Variation.—Little variation is evident among the 17 available specimens. Females as large as 31.2 mm (KU 130315) are immature (small eggs, narrow oviducts). Specimens from the Paso San Juan (northerly locality, Fig. 12C) differ from those from the slopes of the Nevado de Chimborazo in lacking white spots on the flanks (Fig. 12D).

Natural history.—*E. orcesi* has been found beneath rocks and in terrestrial

bromeliads in páramos by day. No data on nocturnal activity are available. On the slopes of Nevado Chimborazo, *E. orcesi* is sympatric with *E. curtipes*. On the crest of the Cordillera Occidental SW of Quito (San Juan area) it is sympatric with *E. curtipes* and *E. unistrigatus*.

In July 1970 the type-series of three individuals was secured under a single rock. In January 1978 I turned over the same rock and found three more individuals. In each instance, a gravid female and a reproductively active male (swollen testes, white nuptial pads) were found.

Distribution.—The Cordillera Occidental of central Ecuador between 3160 and 3800 m (Fig. 16).

***Eleutherodactylus thymelensis* Lynch**

Fig. 12E

Eleutherodactylus whymperi: Lynch, 1971:45, 146.

Eleutherodactylus thymelensis Lynch, 1972:144 (holotype, KU 117719, an adult male obtained in the Páramo del Angél, ca. 23 km [airline] SW Tulcán, Prov. Carchi, Ecuador, 3700 m, by J. D. Lynch on 24 February, 1968).

Diagnosis.—(1) skin of dorsum bearing large, flat granules, that of venter areolate; paravertebral but not dorsolateral folds present; (2) tympanum concealed beneath skin; (3) snout round in dorsal and lateral profiles; canthus rostralis sharp; (4) no cranial crests; no enlarged eyelid tubercles; (5) vomerine odontophores oblique; (6) males with vocal slits, subgular vocal sac; (7) first finger

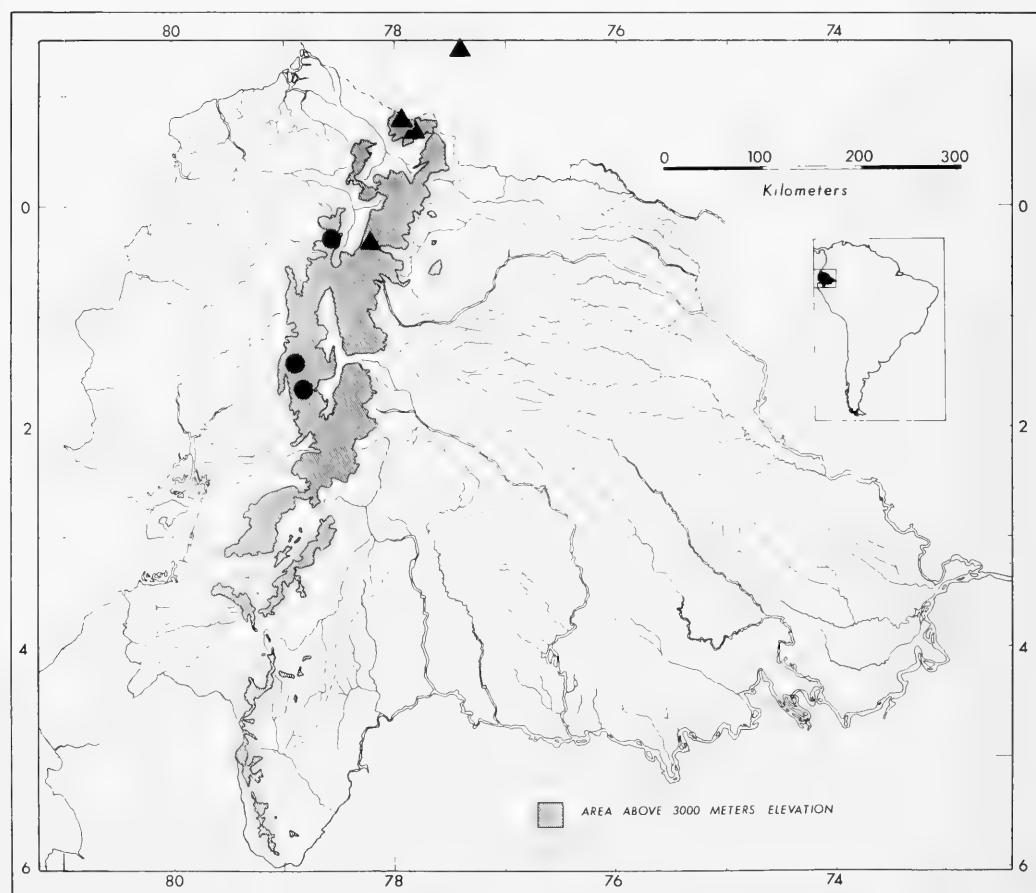


FIG. 16. Distribution of *Eleutherodactylus orcesi* (●) and *E. thymelensis* (▲).

shorter than second; pads and discs present; (8) fingers bear lateral fringes; (9) ulnar tubercles prominent; (10) an inner tarsal tubercle; less prominent tubercles on heel and outer edge of tarsus; (11) two metatarsal tubercles, inner oval, 5-6 times size of outer; numerous supernumerary plantar tubercles; (12) toes bear lateral fringes; toe pads and discs as large as those of fingers; (13) gray to rust-brown above with gray, tan, or black speckling, no color pattern; venter gray to brown, flecked or marbled with black; posterior surfaces of thighs brown; (14) adults small, males 21.4-25.2 ($\bar{x} = 23.6 \pm 0.5$, $N = 18$) mm, females 28.0-33.5 ($\bar{x} = 31.1 \pm 1.4$, $N = 7$) mm SVL.

Eleutherodactylus thymelensis is most similar to *E. obmutescens* from the

Páramo de Puracé but differs in having a vocal sac and vocal slits, an exposed frontoparietal fontanelle, and smaller outer metatarsal tubercle.

Description.—Lynch (1972b).

Natural history.—*E. thymelensis* remains inexplicably rare. Although it was abundant on 23-24 February 1968 when first collected, subsequent efforts at other localities have yielded only four additional specimens. All specimens known were collected by day beneath rocks. Five localities lie in *Espeletia* páramos (Fig. 7A-B) but the locality in Prov. Pichincha lacks *Espeletia* (Fig. 7C-D).

Distribution.—Known from five páramo localities in southern Colombia and northern Ecuador at elevations between 3310 and 4150 (Fig. 16).

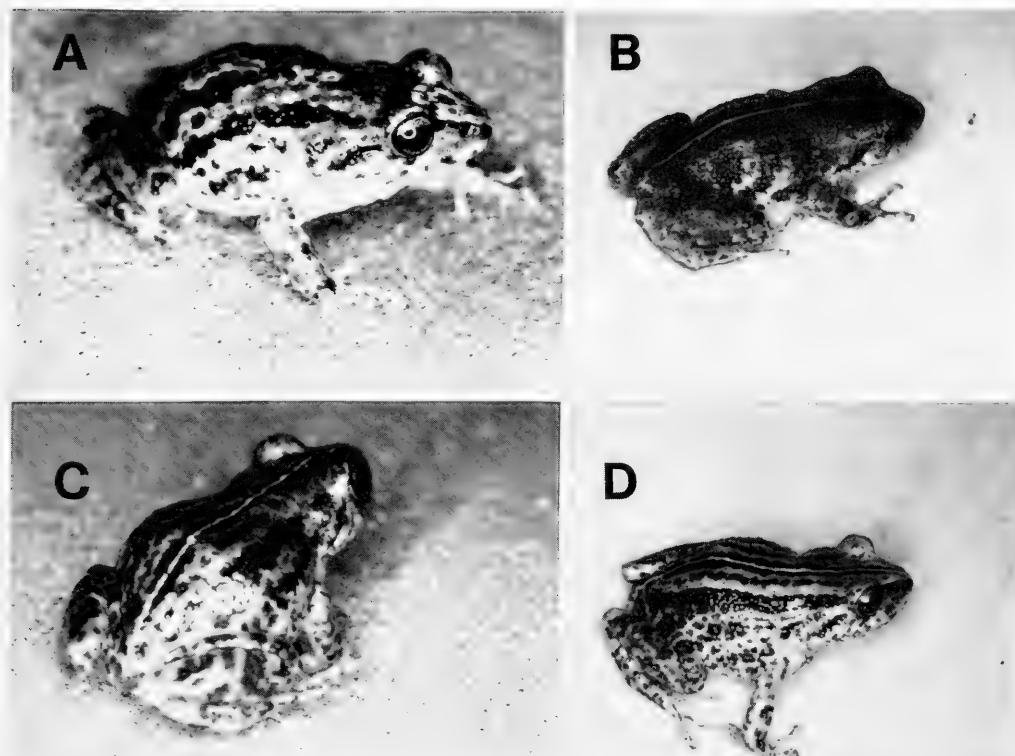


FIG. 17. *Eleutherodactylus unistriatus* pattern morphs. (A) spotted morph, Quito, not preserved; (B) mid-dorsal line morph, KU 177476; (C) striped morph, Quito, not preserved; (D) striped morph, KU 138852.

Eleutherodactylus unistrigatus
 (Günther)
 Figs. 12F, 17

Hylodes unistrigatus Günther, 1859, Proc. Zool. Soc. London, 27:416 (cotypes, BMNH 60.6.16.97(2) and 60.6.16.105 [reregistered as 1947.2.17.7-9] from "western Ecuador" collected by Mr. Fraser).

Hylodes lehmanni Boettger, 1892, Kat. Batr. Mus. Senckenburg. p. 26 (cotypes, Mus. Senckenburg 1200, 1a [not examined], collected by C. F. Lehmann, from the páramo del Bordoncillo, 3500 m [probably along the frontier between Departamento de Nariño and Intendencia Putumayo], Colombia, in 1885). New synonym.

Phyllobates equatorialis Barbour, 1908, Bull. Mus. Comp. Zool., 51:320-21 (cotypes, MCZ 2261, 85082, from "Equator").

Syrphophus coeruleus Andersson, 1945, Arkiv för Zoologi, 37A(2): 24 (syntypes, NHRM 1913 (5 examples), "Eastern Ecuador" collected by Wm. Clarke-Macintyre 1937-1938). New synonym.

Diagnosis.—(1) skin of dorsum shagreened, with scattered flat warts, that of venter aerolate; no dorsolateral folds; (2) tympanum partially concealed, its length $\frac{1}{4}$ - $\frac{1}{3}$ eye length; (3) snout short; snout subovoid to subacuminate in dorsal view, round in lateral profile; canthus rostralis moderately sharp; (4) IOD broader than upper eyelid; no cranial crests; upper eyelid lacking obvious tubercles; (5) vomerine odontophores oblique, moderately prominent (absent in young individuals and some southern populations); (6) males with vocal slits, external subgular vocal sac; small white nuptial pad on thumb of males; (7) first finger shorter than second; pads of outer fingers as broad as tympanum; (8) indistinct lateral fringes on fingers; (9) ulnar tubercles not evident except anteribrachial; (10) no tubercles on heel or outer edge of tarsus; indistinct fold or tubercle on inner edge of tarsus; (11) two metatarsal tubercles, inner oval, 3-4 times size of elongate outer; supernumerary plantar tubercles present, most distinct at bases of toes; (12) toes bear narrow lateral fringes and distinct pads; (13) most pale brown (to cream) above with brown markings (interorbital tri-

angle, dorsal chevrons [scapular, sacral, and suprainguinal], canthal-supratympanic stripe); venter cream; groin finely stippled with brown (or unpigmented); anterior and posterior surfaces of thighs finely stippled with brown; polymorphic—see text; (14) adults small, males 14.9-28.8 mm, females 22.5-38.5 mm SVL; geographically variable, see text.

Eleutherodactylus unistrigatus is most similar to *E. cajamarcensis* and *E. modipeplus* but differs in having the posterior surfaces of the thighs brown with (or without) cream reticulation, in lacking tubercles on the upper eyelid, usually lacking tubercles on the dorsum (present on the flanks), and in having less distinct supernumerary plantar tubercles.

Description.—Head narrower than, to as wide as, body in males, broader than body in adult females, wider than long; snout subovoid to subacuminate in dorsal view, round in lateral profile; nostrils weakly protuberant, directed dorsolaterally; canthus rostralis moderately sharp, straight to weakly concave; loreal region weakly concave, sloping abruptly to lips; lips not flared; interorbital space flat (lacking cranial crests in most individuals, weakly evident in adult females); upper eyelid lacking prominent tubercles; temporal region sloping; supratympanic fold present, obscuring upper edge of tympanum; tympanum visible, not distinct, round in males, higher than long in females, separated from eye by 1-1 $\frac{1}{4}$ tympanum length; postrostral tubercles non-conical; choanae round, small to moderate-sized, not concealed by palatal shelf of maxillary arch; vomerine odontophores usually present, moderately prominent, median and posterior to choanae, oblique (slanted), widely separated medially (1 $\frac{1}{2}$ -2 choanal widths), bearing 0-4 teeth on posterior edge, each odontophore smaller (to equal) than a choana; odontophores less elevated in males (frequently not visible in males); tongue 1 $\frac{1}{2}$ -2 times as long as wide, posterior edge weakly notched, posterior $\frac{1}{3}$ - $\frac{1}{2}$ not adherent to floor of mouth; males with vocal slits

lateral to tongue; external, subgular vocal sac.

Skin of dorsum shagreened with scattered flat warts, that on flanks bearing more numerous warts, that on venter and underside of thighs coarsely areolate; no dorsolateral folds; anal opening not ornamented with tubercles; discoidal folds prominent, well anteriad of groin; upper surfaces of limbs coarsely shagreened; ulnar tubercles not evident except for small, non-conical antebrachial; palmar tubercle bifid (or divided with large inner and small outer), 2 times size of oval thenar tubercle; supernumerary palmar tubercles low, indistinct; subarticular tubercles round, elevated; fingers bearing indistinct lateral fringes; all fingers bearing discs (broader than long) on dilated pads (pads of outer fingers progressively larger than those on inner digits); pads apically rounded to truncate; those of fingers III and IV as large as tympanum; first finger shorter than second.

Knee, heel, and outer edge of tarsus lacking tubercles; inner edge of tarsus bearing indistinct fold on distal $\frac{1}{3}$ (may appear as a tubercle); inner metatarsal tubercle twice as long as wide, not compressed, 3-4 times size of elongate, low outer metatarsal tubercle; supernumerary plantar tubercles numerous, low and indistinct, those at bases of toes II-IV moderately distinct; subarticular tubercles subconical, smaller than those of fingers; toes bearing narrow lateral fringes; toes bearing discs on pads; pads of toes about as large as those of outer fingers; heels of flexed hind limbs touch; heel of adpressed hind limb reaches to tympanum.

The most common coloration and pattern (spotted morph, Pattern A, Table 7) is as follows: pale brown above with indefinite darker interorbital triangle, series of brown spots forming dorsal chevrons (extending onto flanks)—scapular, sacral, and suprainguinal (these spots sometimes nearly black); limb bars nearly transverse, about as broad as paler interspaces; canthal and supratym-

panic stripes dark brown; labial bars indistinct; posterior thigh finely stippled with brown, groin finely stippled with brown or not pigmented; venter cream (very finely stippled with brown), throat of large females sometimes dusky.

A variant (mid-dorsal line morph, Pattern B, Table 7) of the above pattern differs only in having a narrow cream vertebral stripe running the length of the body. Another color pattern (striped morph, Pattern C, Table 7) consists of tan, medium-brown, and dark brown stripes on the back (Fig. 17). In this variant, a thin cream mid-dorsal stripe is usually visible.

Specimens from the Quito-Otavalo and Latacunga areas never have the unpigmented area in the groin. Frogs in the Pasto-Tulcán region usually have the unpigmented areas.

These five northern populations are structurally homogeneous but differ in the frequency of striped morph pattern, size, and testes coloration. Specimens from the Quito-Machachi area uniformly have white testes without gray to brown reticulation (testis color #1, Table 7). Specimens from Otavalo-Cayambe have gray to brown reticulation on white testes (testis color #2, Table 7) or have white testes. Those from Provincia Carchi, Ecuador, and Departamento Nariño, Colombia, usually have brown testes with dark reticulation (or uniformly black testes) (testis color #3, Table 7). Specimens from the vicinity of Latacunga resemble those from Otavalo. Females from Prov. Carchi, Ecuador, and Depto. Nariño, Colombia, frequently have pigmentation of the mesentary covering the ovaries.

The striped morph is less common in collections from Quito than from elsewhere in northern Ecuador and southern Colombia (Table 7). The highest frequency of striped frogs is in extreme northern Ecuador but this may reflect small samples. Two subsamples from Carchi Province have 28.6 and 53.3% striped individuals respectively (N of 14 and 15). Four subsamples from De-

partamento de Nariño include 8.7, 12.0, 12.9, and 53.8% striped frogs. Four subsamples from Otavalo include 9.1, 12.9, 14.7, and 17.5% striped frogs. These contrast with three subsamples from Quito of 3.0, 4.3, and 14.0% striped frogs. The striped morph of *E. unistriatus* was confused with *E. buckleyi* by Boulenger (1882: pl. 14, fig. 5) who unfortunately illustrated this cotype (BMNH 78.1.25-42), an action which led Peracca (1904) to report at least two species having a similar morph as *Hyloides buckleyi*.

In life, *E. unistriatus* is pale yellow-brown to medium brown or terra cotta (if brown, often with terra cotta blotches dorsally); dorsum spotted with darker brown and/or black; flanks creamy brown flecked with brown; limbs same color as dorsum, sometimes slightly more pale; some specimens have creamy yellow flecks superimposed on pattern; throat of male bright yellow, venter yellow-white; in females, throat flesh-colored and/or flecked with brown, venter white; posterior surfaces of thighs a pale version of dorsum, yellowish in males; iris gray-bronze to silvery, with many black flecks, dark brown horizontal streak.

Variation.—In addition to the variation in color patterns and testes color, *E. unistriatus* exhibits geographic variation in body size (Table 7). Males from extreme northern Ecuador and adjacent Colombia are markedly smaller than males from other areas in Ecuador. The trend is not so evident among females because female *E. unistriatus* from Quito are small. In general, the largest individuals come from those populations in the Ambato-Latacunga *hoya*.

Specimens from 5-10 km W Baños, Prov. Tungurahua, are distinctive in their smaller tympana (Table 8) and because the vomerine odontophores are very indistinct (scarcely elevated). These frogs have odontophores (at least on one side, if not both, but very few teeth [0-2/odontophore]. The posterior surfaces of the thighs are cream marbled with brown. The skin is more pustulose

than that seen in most populations of *E. unistriatus*.

Geographic variation in *E. unistriatus* is more gradual than in *E. curtipes*. Adjacent populations do not exhibit markedly different proportions or coloration (Tables 7-8) This can be explained in that populations of *E. unistriatus* are more contiguous than are populations of *E. curtipes*.

Natural History.—As mentioned in the account for *E. modipeplus*, *E. unistriatus* breeds between December and February. Calling males can be heard from Tulcán to Riobamba below elevations of 3200 m. In January, 1978, I drove from Quito to Otavalo and in mesic areas heard an unbroken chorus of *E. unistriatus*, occasionally joined by enclaves of *Gastrotheca riobambae*. Development of *E. unistriatus* was described by Nina and del Pino (1977). In spite of having collected thousands of individuals of this frog, I have found only a single egg mass. KU 180302 was found 18 January 1978 under a clod of dirt 6.9 km SE San Rafael, Prov. Imbabura, 2900 m. The embryos, in an advanced stage of development (large fan-like tail, limbs well developed), were in a small cavity $2 \times 2 \times 1$ cm with no avenue of access into the clutch. The 17 eggs were not adherent.

Young frogs are abundant in June in Quito but only adults are encountered in December. Presumably the frogs mature in a single year.

The seasonality of reproduction is marked. I heard no calling males in June through August, even in pastures in cloud forests (e.g., Pilaló or El Carmelo). This seasonality makes sense in the relatively arid interandean valleys but is striking when duplicated in cloud forests. The population of *E. unistriatus* at Pilaló, Provincia Cotopaxi, Ecuador, 2400 m, is isolated from the contiguous populations in the interandean valleys of Ecuador by the páramos de Apaqua but in mid-January 1978, *E. unistriatus* was calling throughout the pastures and cleared areas in the vicinity of Pilaló.

TABLE 7. Geographic variation in body size, color pattern, and color of testes in *Eleutherodactylus unistriatus*.

Locality	Males	Females	Pattern			(N)	Testes		
			A	B	C		1	2	3
Dept. Nariño	17.7-23.6(17) ¹ 20.2±0.8	24.0-31.1(26) 28.1±0.7	76.8	3.6	19.6	(138)	3	0	9
Prov. Carchi	14.9-23.2(25) 18.8±0.8	23.3-30.8(46) 26.3±0.4	55.2	3.4	41.4	(29)	3	13	9
Otavalo	20.5-25.6(26) 22.7±0.6	26.5-34.7(32) 30.4±0.7	77.6	7.2	15.2	(290)	7	17	2
Cayambe	----	----	78.8	1.9	19.2	(52)	---	---	---
Quito	17.7-28.8(39) 22.1±0.8	22.5-32.7(61) 27.7±0.6	92.2	0.0	7.1	(170)	41	0	0
Machachi	----	----	81.8	0.0	18.2	(11)	---	---	---
Latacunga	18.0-28.1(12) 24.8±1.4	24.8-35.2(23) 30.7±1.2	85.7	0.0	14.3	(35)	3	7	1
Pilaló	14.5-24.0(46) 19.1±0.7	23.0-31.0(22) 26.8±0.9	65.8	0.0	34.2	(79)	35	5	6
Ambato	19.3-28.5(49) 24.8±0.6	26.8-38.5(49) 31.9±0.8	92.7	0.0	7.3	(82)	17	2	9
W of Baños	20.2-23.9(9) 22.6±1.0	27.4-33.9(18) 30.2±0.9	100.0	0.0	0.0	(27)	15	0	9
Riobamba	20.2-28.2(20) 22.6±0.8	24.7-35.7(20) 29.8±1.4	100.0	0.0	0.0	(45)	---	---	---
Pungalá	----	----	100.0	0.0	0.0	(38)	---	---	---

¹ First line, range (N); second line $\bar{x} \pm 2SE$.TABLE 8. Proportions of *Eleutherodactylus unistriatus*. First line, range (N); second line, mean $\pm 2SE$.

Locality	Shank/SVL	HW/SVL	Eyelid/IOD	Tympanum/Eye	E-N/Eye
Nariño ♀	40.3-46.5(15) 42.4±1.0	34.9-38.6(15) 37.2±0.5	75.8-100.0(14) 91.0±3.7	29.0-44.1(14) 37.7±2.3	76.5-91.2(15) 84.7±2.5
Otavalo ♂	43.4-44.7(5) 44.0	35.9-39.0(5) 37.8	74.1-96.0(5) 83.0	37.5-44.4(5) 40.5	84.6-91.3(5) 86.9
Quito ♂	40.0-45.7(13) 42.7±1.0	30.8-39.1(13) 36.8±1.1	67.3-100.0(13) 88.5±5.1	33.3-52.0(13) 42.2±3.0	76.9-92.0(13) 82.4±2.4
Quito ♀	39.9-44.2(17) 41.6±0.6	35.1-39.5(17) 37.0±0.6	71.0-90.3(16) 81.7±2.7	32.7-51.7(17) 43.7±2.8	71.0-100.0(17) 88.1±3.2
Ambato-Riobamba ♂	42.2-47.2(20) 44.3±0.6	35.6-39.4(20) 37.3±0.4	65.7-90.5(20) 78.9±3.1	34.0-50.0(20) 43.7±1.8	76.7-88.5(10) 82.7±2.4
5-10 km W Baños ♂	41.6-48.5(20) 44.7±0.8	34.8-38.7(20) 36.7±0.5	60.0-88.0(20) 74.4±3.1	43.0-58.3(20) 50.0±1.9	77.8-93.3(11) 85.3±2.8
5-10 km W Baños ♀	42.4-48.3(9) 44.5±1.2	33.2-37.2(9) 35.0±0.8	69.2-92.0(9) 83.0±4.3	23.1-38.7(9) 30.1±3.5	71.0-84.6(9) 78.3±3.3
5-10 km W Baños ♀	41.7-49.1(18) 44.9±1.0	32.8-38.2(18) 35.8±0.6	80.0-116.7(17) 91.2±4.4	24.2-41.4(18) 34.5±2.3	73.0-100.0(18) 85.0±3.0

The call is a hollow click. To my ear, it sounds like the noise produced by rapping two hollow bamboo tubes together and is very much unlike the whistle of *E. modipeplus*.

During the day, *E. unistriatus* is concealed, usually beneath objects on the ground (rocks, logs, boards, trash, grass), but individuals have also been found in terrestrial bromeliads, and in arboreal bromeliads (up to 3 m high in trees at Lago Cuicocha). At night, individuals are found on vegetation as well as on the ground. Calling males perch on vegetation to at least 1 m above the ground. Lynch (1969, 1970) described microhabitat differences between sexes (at least during breeding activity).

In interandean Ecuador (Fig. 18), *E. unistriatus* is most abundant between 2500 and 3200 m, but has been collected as high as 3490 m (Nudo de Tiopullo, Prov. Cotopaxi, Ecuador). The contiguous interandean populations enter the

upper Pastaza Trench (as low as Baños, 1800 m). At least three, presumably isolated populations occur on the Andean slopes. The Pilaló (2400 m) population was cited above. A second population (Mindo-Nono area, 1500-2530 m) is found in Provincia Pichincha. The third occurs in extreme northern Ecuador (El Carmelo 2710 m, Prov. Napo). This population may be contiguous with interandean populations across the low (3200) *frailejon* (*Espeletia*) páramo de las Juntas SE of Túcán.

Remarks.—Barbour and Noble (1920) pointed out that *Phyllobates equatorialis* Barbour is a synonym of *E. unistriatus*. *Hylodes lehmanni* Boettger and *Syrrophus coeruleus* Andersson are also synonyms of *E. unistriatus*. *Hylodes lehmanni* is founded on a striped morph of *E. unistriatus*. Except for the color pattern, this morph is identical to the more common spotted morph. Cochran and Goin (1970) emphasized the striped

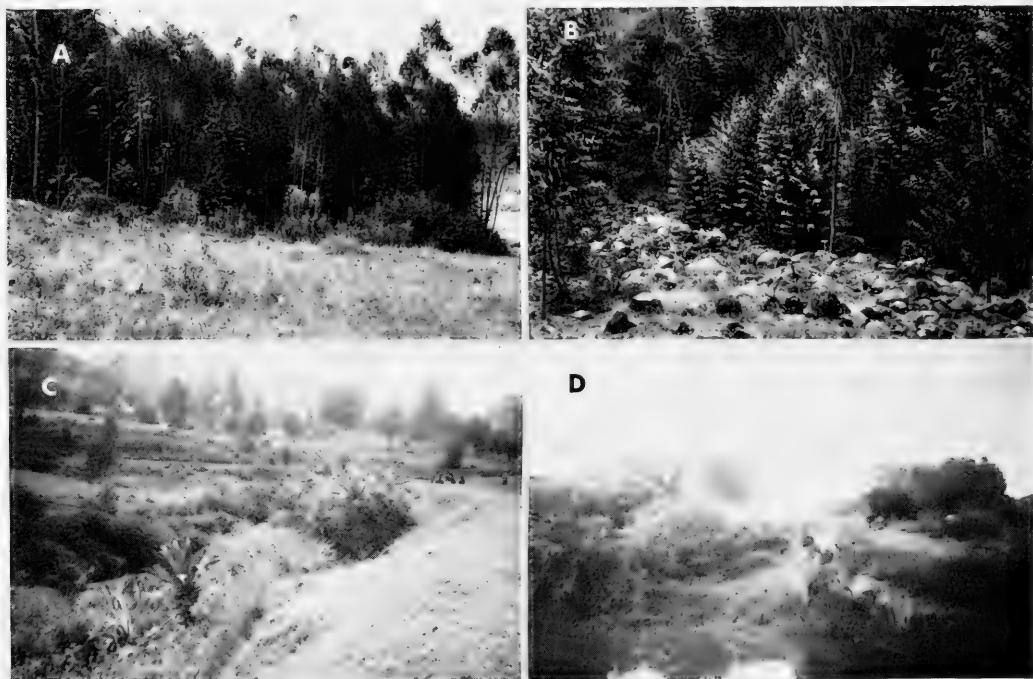


FIG. 18. *Eleutherodactylus unistriatus* habitats. (A, B) Aspect and detail of *Eucalyptus*-pasture habitat, 3 km SSW San Miguelito, Prov. Tungurahua, 2620 m; (C) pasture, 1 km N Otavalo, Prov. Imbabura, 2560 m; (D) brickyard in west Quito—*E. unistriatus* was abundant around the pond and in other mesic microhabitats at this site in 1967.

pattern in their description of *E. lehmanni* but in no subsample of specimens from Pasto region does the frequency of the striped morph exceed 54%. The largest specimen I have seen from Colombia is USNM 146232 (31.1 mm). Boettger (1892) reported the larger cotype to be 33 mm SVL and to have a spotted belly. The specimens reported by Cochran and Goin (1970) from Departamento de Caldas, Colombia (including the example 37 mm long) are striped specimens of an ally of *E. vertebralis* (Boulenger), *E. supernatis* Lynch.

Syrrhophus coeruleus Andersson is based on five individuals I believe to be conspecific with the material from 5-10 km W Baños, Prov. Tungurahua, Ecuador. In these frogs vomerine teeth and odontophores are poorly developed and the posterior surfaces of the thighs are marbled with brown. Based on brief color notes by the late James A. Peters and my study of the preserved specimens, I tentatively assign them to *E. unistriatus*. However, study of living specimens may reveal this to be a distinct species, in which case Andersson's name is available.

The situation in interandean Ecuador in the Baños—Ambato region and on the surrounding andean spurs is suggestive of confounding of two or more species. In addition to *E. modipeplus* and *E. unistriatus* (essentially identical to specimens from Quito), the *coeruleus*-like frogs, and *E. pastazensis* Andersson (see Lynch and Duellman, 1980, for redescription) occur in this restricted region. Specimens from 7-10 km W Baños include frogs with small white testes and frogs with large black testes. Correlated (partially) with the differences in testes color, are relative distinctness of the tympana, skin texture, distinctness of marbling on the posterior surfaces of the thighs, and duskiness of the venter. I am reluctant to propose additional names until the localities have been recollected, colors in life recorded from fresh material, and acoustical data are available.

Distribution.—The Nudo de Pasto in Colombia south to Riobamba in Ecuador through the interandean valleys. Isolated and semi-isolated populations on the andean flanks in northern and central Ecuador (Fig. 9).

DISCUSSION

The elutherodactyline fauna of high altitude habitats of southern Colombia and northern Ecuador is impoverished compared with that of southern Ecuador (Lynch, 1979). The northern fauna essentially consists of three species—*E. buckleyi*, *E. curtipes*, and *E. unistriatus*. The other six species (*E. modipeplus*, *E. myersi*, *E. ocreatus*, *E. orcesi*, *E. thymelensis*, and *Phrynobatrachus brunneus*) are rare species having small distribution areas. All eight *Eleutherodactylus* are species of the *unistriatus* group as defined by Lynch (1976) and represent four assemblies within that group:

curtipes assembly—*E. buckleyi*, *E. cryophilus*, and *E. curtipes* are very similar frogs whose distributions tend to replace one another (Fig. 19).

myersi assembly—*E. ginesi* (Rivero), *E. myersi*, *E. nicefori* Cochran and Goin, *E. ocreatus* Lynch, *E. orestes* Lynch, *E. trepidotus* Lynch, and *E. vidua* Lynch form a series of species characterized by their minute digital pads. This assembly is distributed primarily on the eastern Cordillera (Fig. 20).

orcesi assembly—*E. obmutescens* Lynch, *E. orcesi* Lynch, *E. racemus* Lynch, *E. simoterus* Lynch, and *E. thymelensis* Lynch form a series of five allopatric populations on the Cordillera Central of Colombia and Cordillera Occidental of Ecuador (Fig. 21).

unistriatus assembly—*E. cajamaricensis* Barbour and Noble and *E. versicolor* Lynch in southern Ecuador, *E. modipeplus* Lynch, *E. pastazensis* An-

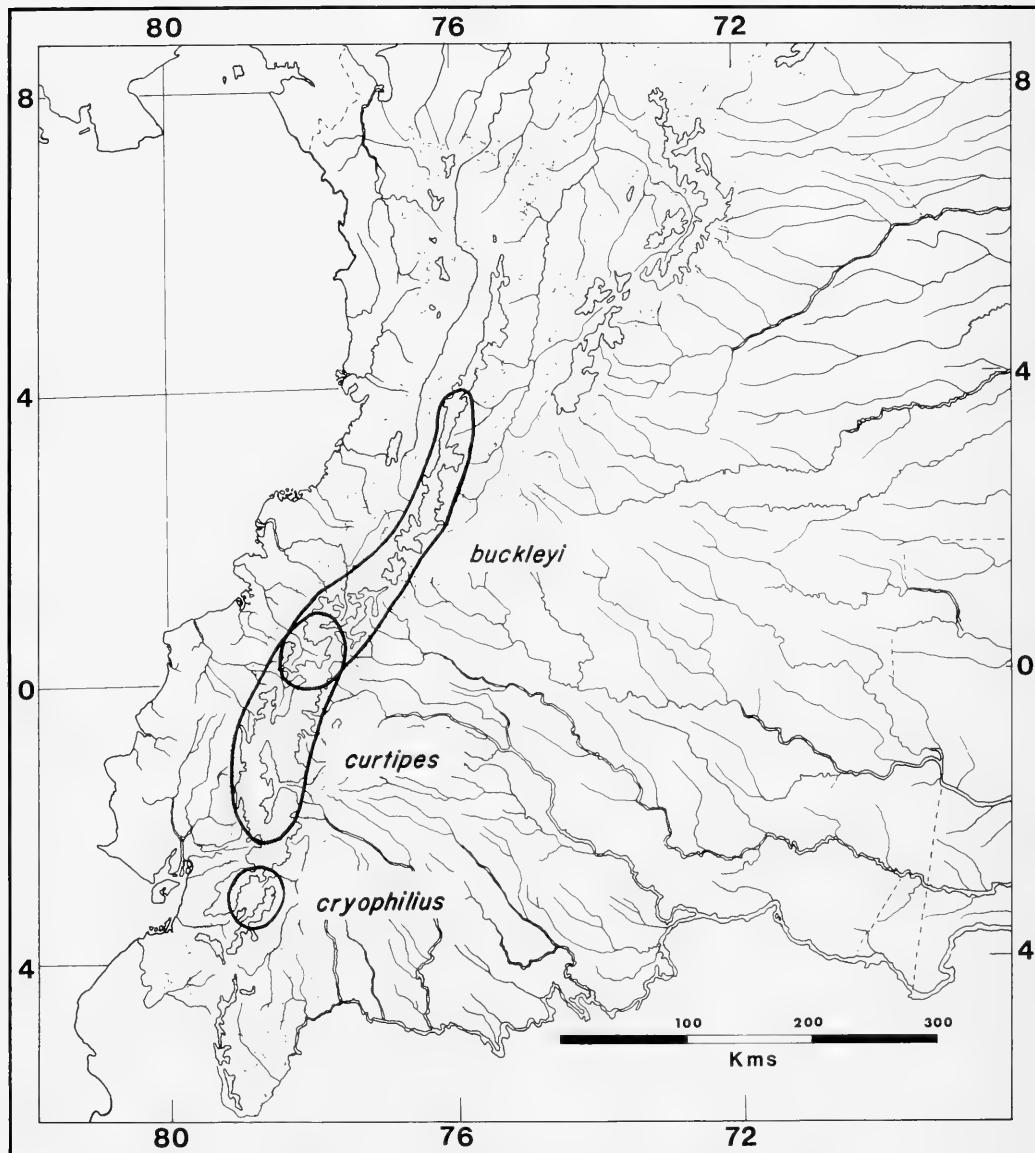


FIG. 19. Distribution of the *curtipes* Assembly (*buckleyi*—*curtipes*—*cryophilus*).

dersson, and *E. unistrigatus* (Günther) in southern Colombia and northern Ecuador, and *E. bogotensis* (Peters) and *E. lynchii* Duellman and Simmons on the Cordillera Oriental in Colombia (Fig. 22).

Two distributional patterns are apparent. The first, involving the species of the *curtipes* and *orcesi* assemblies, involves distribution along the Cordillera

Occidental of Ecuador and the Cordillera Central of Colombia, whereas the *myersi* and *unistrigatus* assemblies are displaced eastward. The second is a pattern of allopatric and disjunct distribution of pairs of relatives (*E. bogotensis* - *E. lynchii* in Colombia; *E. ocreatus* - *E. trepidotus* in northern Ecuador; *E. cryophilus* - *E. curtipes* in central Ecuador; *E. ginesi* - *E. niceforoi* in Colom-

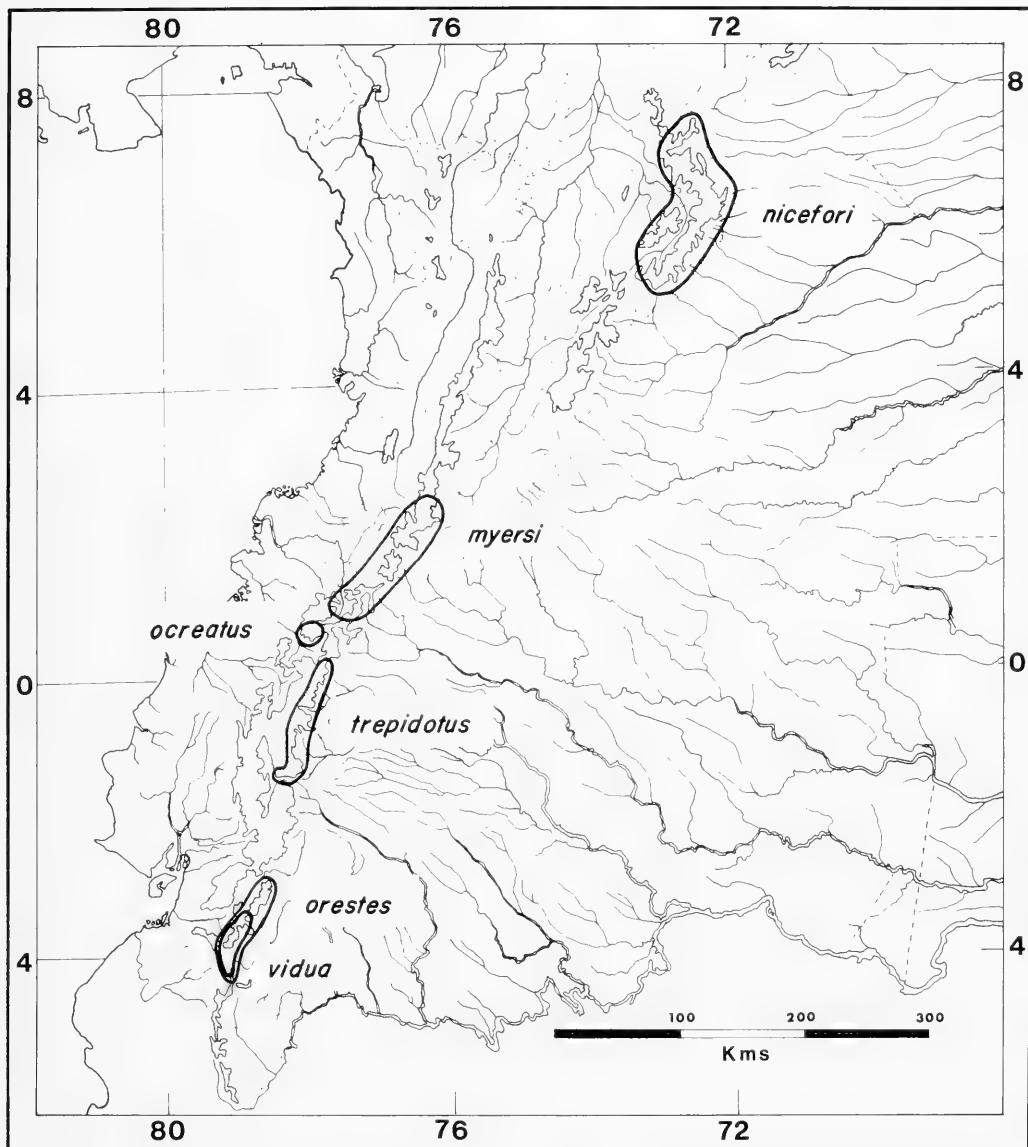


FIG. 20. Distribution of the *myersi* Assembly in Colombia and Ecuador (*nicefori*—*myersi*—*ocreatus*—*trepidotus*—*orestes*—*vidua*).

bia and Venezuela; the five species of the *oresti* assembly) and is contrasted to the less common partial ecologic-geographic separations as seen in *E. buckleyi* - *E. curtipes*, *E. cajamarcensis* - *E. versicolor*, *E. modipeplus* - *E. unistrigatus*.

Most of the species of these four assemblies are inhabitants of cool, moist environments. The two exceptions, *E.*

pastazensis and *E. unistrigatus*, are related. The former is poorly known (Lynch and Duellman, 1980). The distribution of *E. unistrigatus* is most profitable contrasted with that of *E. curtipes* (Figs. 8-9). The two are sympatric at only 10 localities, ranging in altitude from 2750 to 3450 m. The relatively lower sites (Tulcán, Machachi, Latacunga) are very wet sites and the mois-

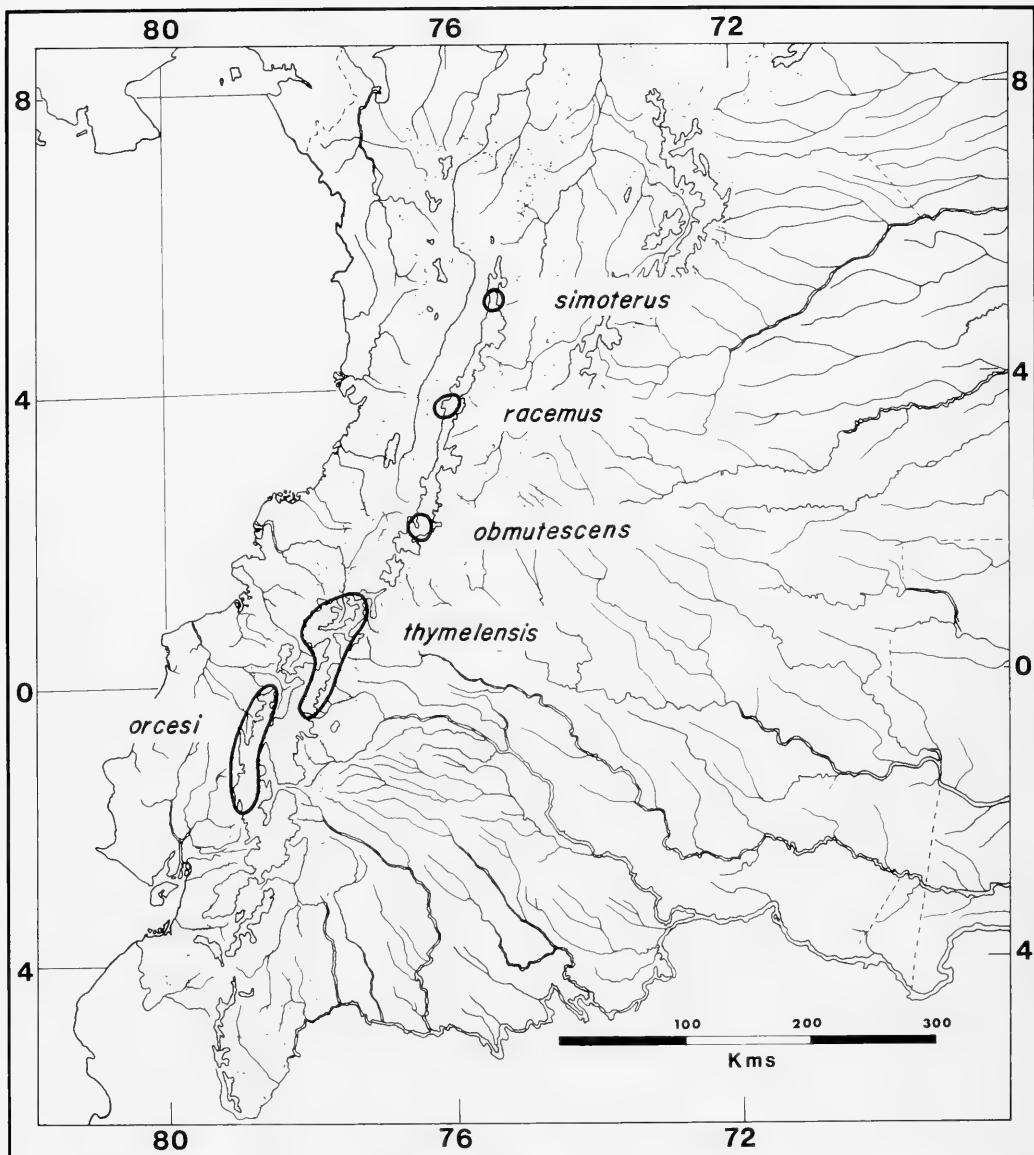


FIG. 21. Distribution of the *orcesi* Assembly (*simoterus*—*racemus*—*obmutescens*—*thymelensis*—*orcesi*).

ture seemingly allows the less common *E. curtipes* to survive there. At the higher sites (13 km SSE Tulcán, Intag, San Juan, Páramo de Tiopullo, 10 km W Cotaló), *E. unistrigatus* was the less common. Higher altitudes may provide too cool an environment for reproduction for *E. unistrigatus*.

The geographic variation in *E. uni-*

strigatus (relatively uniform cline) contrasts with that seen in *E. curtipes* (punctuated clines). These discordant patterns of geographic variation seem consistent with the notion that the distribution of *E. unistrigatus* was recently contiguous and is only now fragmenting whereas that of *E. curtipes* is now expanding towards contiguity.

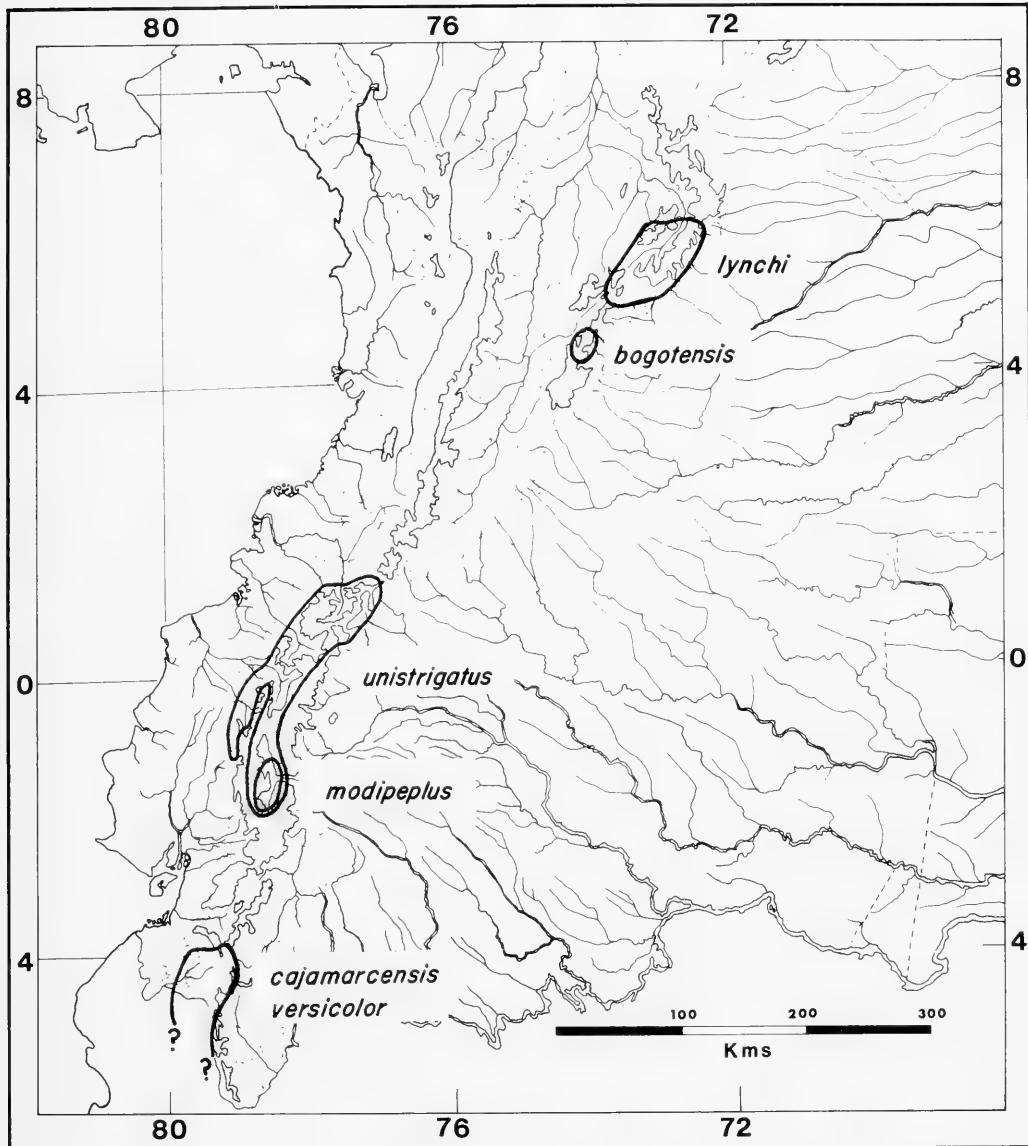


FIG. 22. Distribution of the *unistrigatus* Assembly (*lynchi*—*bogotensis*—*unistrigatus*—*modipeplus*—*cajamarcensis* and *versicolor*).

SUMMARY

The páramos and subpáramos of northern Ecuador and southern Colombia are populated by eight species of *Eleutherodactylus*. The most widely distributed species are *E. buckleyi*, *E. curtipes*, and *E. unistrigatus*. *Eleutherodactylus modipeplus* new species, *E. myersi*,

E. ocreatus new species, *E. orcesi*, and *E. thymelensis* have smaller distribution areas. Two new species are named, *E. modipeplus* from montane regions near Ambato, Ecuador, and *E. ocreatus* from the páramo del Angéł west of Tucán, Ecuador. *Hylobates whympéri* and *Hyla*

chimboe are considered synonyms of *Eleutherodactylus curtipes*. *Hylodes lehmanni* and *Syrrhopus coeruleus* are considered synonyms of *Eleutherodactylus unistriatus*.

The eight species of *Eleutherodactylus* are members of the dominant *curtipes* group and are sorted into four assemblies. The *curtipes* assembly (*E. buckleyi*, *E. cryophilus*, and *E. curtipes*) and the *orcesi* assembly (*E. obmutescens*, *E. orcesi*, *E. racemus*, *E. simoterus*, and *E. thymelensis*) are distributed on the Cordillera Central of Colombia and in the northern Andes of Ecuador whereas the *myersi* assembly (*E. ginesi*, *E. myersi*, *E. nicefori*, *E. ocreatus*, *E. orestes*, *E. trepidotus*, and *E. vidua*) and the *unistriatus* assembly

(*E. bogotensis*, *E. cajamarcensis*, *E. lynchi*, *E. modipeplus*, *E. pastazensis*, *E. unistriatus*, and *E. versicolor*) are distributed on the Cordillera Oriental of Colombia (and one assembly extends onto the Venezuelan Andes) and the Cordillera Real of Ecuador (to the Huancabamba depression).

The two distribution patterns for assemblies may reflect the same dynamic interaction seen between two widely distributed Ecuadorian species (*E. curtipes* and *E. unistriatus*). *Eleutherodactylus curtipes* is distributed at higher altitudes than *E. unistriatus* and appears to be in the process of range expansion whereas *E. unistriatus* appears to be experiencing range fragmentation.

RESUMEN

Ocho especies de *Eleutherodactylus* se encuentran en los páramos y subpáramos del norte de Ecuador y de Colombia meridional. Las especies con distribuciones amplias son: *E. buckleyi*, *E. curtipes*, y *E. unistriatus*. *Eleutherodactylus modipeplus* (especie nueva), *E. myersi*, *E. ocreatus* (especie nueva), *E. orcesi*, y *E. thymelensis* tienen distribuciones menores. Se nombran dos especies nuevas, *E. modipeplus*, de las regiones altas cerca Ambato, Ecuador, y *E. ocreatus*, del páramo del Angélico al oeste de Tulcán, Ecuador. *Hylodes whymperi* y *Hyla chimboe* son considerados sinónimos de *Eleutherodactylus curtipes*. *Hylodes lehmanni* y *Syrrhopus coeruleus* son sinónimizados con *Eleutherodactylus unistriatus*.

Las ocho especies de *Eleutherodactylus* son miembros del grupo *unistriatus* (el grupo más dominante en esta parte de América del Sur) y se asignan a cuatro asambleas (= subgrupos del grupo *unistriatus*). La asamblea *curtipes* (*E. buckleyi*, *E. cryophilus*, y *E. curtipes*) y la asamblea *orcesi* (*E. obmutescens*, *E. orcesi*, *E. racemus*, *E.*

simoterus, y *E. thymelensis*) se encuentran en la Cordillera Central de Colombia y los Andes al norte de Ecuador, mientras que la asamblea *myersi* (*E. ginesi*, *E. myersi*, *E. nicefori*, *E. ocreatus*, *E. orestes*, *E. trepidotus*, y *E. vidua*) y la asamblea *unistriatus* (*E. bogotensis*, *E. cajamarcensis*, *E. lynchi*, *E. modipeplus*, *E. pastazensis*, *E. unistriatus*, y *E. versicolor*) se encuentran en la Cordillera Oriental de Colombia (y una especie también se encuentra en los Andes venezolanos) y la Cordillera Real de Ecuador (hasta la depresión de Huancabamba).

Los dos modelos de distribución para las asambleas posiblemente reflejan la misma acción recíproca dinámica que se ve en las dos especies ecuatorianas con amplias distribuciones (*E. curtipes* y *E. unistriatus*). *Eleutherodactylus curtipes* se encuentra en alturas mayores que *E. unistriatus* y parece estar en proceso de expandir su distribución mientras que *E. unistriatus* se encuentra en sitios más bajos y su distribución aparentemente está contrayéndose.

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APPENDIX: SPECIMENS EXAMINED

Eleutherodactylus buckleyi (255 spec.)

COLOMBIA, Depto. Cauca: Páramo de las Papas, MLS 144; Páramo de Puracé, 3400 m, KU 145018; Páramo de Puracé, Laguna de San Rafael, 3200 m, ICN 1539, 1549-55, 2082-84, 2086, 2088, 2090, 2599, KU 143896-933, UMMZ 166582, UVMP 794-800; 17 km E Puracé, 3300 m, KU 167904-16, 168431, WED

42427-28; 18 km E Puracé, Río Cocuy, 3320 m, KU 167903; 19 km E Puracé, 3420 m, KU 167918-23, 170167; 23 km E Puracé, 3275 m, KU 167924-30, 170125-26 (CS); 26 km E Puracé, 3130 m, KU 167931-44; 30 km E Puracé, 3030 m, KU 167945-48. Depto. Huila: Hda. Meremberg, Santa Leticia, 2400 m, ICN 2576. Depto. Nariño: ca. 4 km N Laguna de la Cocha, 3200 m, AMNH 86755-60; Páramo

El Tabaño, 3200 m, ICN 2498-99, 2502, 2504; Municipio de Pasto, lado norte del Volcán Galeras, 3310 m, UVMP 2867, 2870; 8 km NE Pasto, 3020 m, KU 167949-50; 12 km E Pasto, 3050 m, KU 167951-56, WED 42816-19; 4 km S Pasto, UVMP 2881; Tuquerres, 3000 m, KU 138724. *Intend. Putumayo*: 13 km W Santiago, 2900 m, KU 167957-58; 16 km W Santiago, 3230 m, KU 167959-60. *Dept. Valle (de Cauca)*: Páramo de las Hermosas, 3570 m, KU 167965; 7 km NE Tenerife, 2850 m, KU 167961; 13 km NE Tenerife, 3310 m, KU 167962-63; 15 km NE Tenerife, 3460 m, KU 167964.

ECUADOR, *Prov. Carchi*: El Carmelo, 2713 m, USNM 204745-47; 10 km (airline) WNW El Carmelo (= 10 km SSE Tulcán), 3201 m, USNM 204742-44, 204748-53; 5.7 km NW El Carmelo, 2910 m, KU 177235-41; 10.8 km NW El Carmelo, 3050 m, KU 177231-34; 14.6 km NW El Carmelo, 3130 m, KU 177226-30; Tulcán, 2770 m, KU 177225; 13 km SSE Tulcán, 3018 m, USNM 204733-41; 14 km SW Tulcán, 3340 m, KU 165150-58, 23 km SW Tulcán, 3700 m, KU 117558-66. *Prov. Imbabura*: Intag, BM 78.1.25.40-41, 78.1.25.43; Urcusiquí, 3300-3500 m, KU 117492-515. *Prov. Napo*: Laguna San Marcos, ± 10000 feet, CAS-SU 8288-99; Santa Barbara, 2591 m, MCZ 92500-01, USNM GOV 7168-70, 7218, 8547, 8551-52, 8554.

Eleutherodactylus curtipes
(1388 spec. + 7 lots of eggs)

ECUADOR, no other locality, MNHNP 06-276. *Prov. Bolívar*: Arenal, 3 km SW frontier on Ambato-Guaranda road, 4000 m, KU 130521-25; Arenal, 6 km SW frontier on Ambato-Guaranda road, 3800 m, KU 130526-43, 177800-01; 16-19 km E Guaranda, 3500-3800 m, KU 130466 (lot of eggs), 130467-519; Guanajo, 2923 m, KU 177802; mountains above San José del Chimbo, 3049-3293 m, ANSP 18137 (holotype of *Hyla chimboe*); Sinche (= Sinchig), 7 leagues E Guaranda, 4000 m, BM 99.10.30.38-40. *Prov. Carchi*: 10 km WNW El Carmelo, 3201 m, USNM 211575-80; 14.6 km NW El Carmelo, 3130 m, KU 177748-54; Tulcán, 2770 m, KU 177736-41, MZS 8653-54; 14 km SW Tulcán, 3340 m, KU 165270-92; 20 km SW Tulcán, 3350 m, KU 165243-69; W slope Volcán Chiles, 10 km W Tufiño, 3500-3600 m, KU 117556-57, 118107 (lot of eggs). *Prov. Chimborazo*: 9 km S Cajabamba, 3260 m, KU 165241-42; 12 km SW Cajabamba, 3800 m, KU 119633-56; Desierto de Palmira, near Palmira, 3110 m, KU 165239-40; 20 km E Guaranda, 3811 m, USNM 211581-82; Guallabamba, 3500 m, BM 99.10.30.35-37; 15 km SE Pungalá, Hda. Alao, 3100 m, KU 130591-94; near Rosario, 3500 m, BM 1932.10.2.54; 10 km W San Juan, 3400 m, KU 119573-632;

Tortorillas, 4024 m, BM 82.7.13.4-5/RR 1947.2.17.22-23 (cotypes of *Hylobates whymperi*); Urbina, 3609 m, KU 130596-640, UMMZ 132902(8), USNM 211583-609. *Prov. Cotopaxi*: Guilo, Páramo de Apagua, 8 km E Pilaló, 3500 m, KU 131357-402; Latacunga, 2750 m, KU 177743; Páramo de Apagua, 3800-3860 m, KU 131334-56, 131696; Páramo de Milín, 3900 m, KU 119682-715; Páramo de Tigua, 3450 m, KU 130465; Páramo de Tiopullo, 3490 m, KU 130753-830; slopes of Volcán Cotopaxi, 3620-3750 m, KU 123492-94. *Prov. Imbabura*: Cotocachi, 3963 m, BM 82.7.13.3/RR 1947.2.17.24 (cotype of *Hylobates whymperi*); Intag, BM 78.1.25.29-36 (cotypes of *Hylobates curtipes*); Lago Cuicocha, 3010 m, KU 177742; Nudo de Mojanda, 3400-3440 m, KU 130726-51; Nudo de Mojanda, 3650-3680 m, KU 130648-724. *Prov. León*: Satacunga, UMMZ 55522 (this locality is probably Latacunga, Prov. Cotopaxi; León was the older name for Prov. Cotopaxi). *Prov. Napo*: east slope, Paso Guamaní, 3950 m, KU 165376-400, 3650 m, KU 109009-58; 10 km W Papallacta, 3610 m, KU 110804-44; 9 km W Papallacta, 3800 m, MCZ 90018; 5 km W Papallacta, 3232-3400 m, KU 110845-90, 177746-47, 180286-89 (lots of eggs), USNM 211717-800; Laguna Papallacta, 3330-3350 m, KU 108990-9008, 165293-375, WED 47707-11, MCZ 95556-58; 1 km W Papallacta, 3155-3200 m, KU 110891-95, USNM 211695-716 + 2 without tags; 2.7 km NW Papallacta, 3300 m, MCZ 91913-30; 18.9 km NW Papallacta, road to Pifo, 3880 m, MCZ 91931-37; Papallacta, 3110 m, UIMNH 55898-915, 55918-21, USNM 211693-94; 3 km E Papallacta, 2900 m, KU 117567-69. *Prov. Pichincha*: MCZ 3021-22; 6-7 km W Chillogallo, ca. 3000 m, UMMZ 132905 (21); Machachi (Universidad Católica Quito); 17 km E Pifo, Paso Guamani, 3800 m, KU 110794-803; trib. Río Pita, N base Cerro Ingalamá, 3780 m, KU 123495-500; 3 km SW Quito, 3200 m, USNM 211688-92; San Juan, 3400 m, KU 177744-45; Volcán Pichincha, 3400-3800 m, KU 130831-69; W slope Volcán Pichincha, 4400 m, CAS-SU 10628. *Prov. Tungurahua*: Arenal, 2 km NE frontier on Ambato-Guaranda road, 3900 m, KU 130520; 7 km W Baños, 2805 m, USNM 211661-82; 8 km W Baños, 2805-2927 m, USNM 211657-60; 10 km W Baños, 2927-3049 m, USNM 211610-56; 10 km W Cotaló, 3300 m, KU 130641-47; 10-10.5 km SSW Mocha, 3450-3480 m, KU 177755, 177757-99, 180290 (lot of eggs), 180291 (4); 10 km SW Mocha, 3700 m, KU 119657-81; 12 km SW Santa Rosa, 3400 m, KU 130566-90; 18 km SW Santa Rosa, 3600 m, KU 130556-65; 20 km SW Santa Rosa, 3700 m, KU 130544-55; 10 km N Urbina, Puente de Mallo, 2974 m, USNM 211683-85, JAP 6432; 12 km N Urbina, USNM 211686-87.

The following are surely the product of

data confusion: FMNH 196028-29, 196035, 196037-38, 196041-42, 196044-45, 196047, 196050-51, 196053-54, 196056-59, purportedly from Bogotá, Depto. Cundinamarca, Colombia, but probably from the vicinity of San José (Chillogallo to Chiriboga road), Prov. Pichincha, Ecuador [the Field Museum has a series of *E. bogotensis* catalogued as having originated from Ecuador; both series of specimens were purchased from E. H. Taylor].

Eleutherodactylus modipeplus (43 spec.)

ECUADOR, Prov. Chimborazo: Guallabamba, 3500 m, BM 99.10.30.41-43; 1 km S Urbina RR station, 3650 m, KU 131283-85. Prov. Tungurahua: 8.1 km S on Baños-Riobamba road, 2560 m, KU 141296; 10.9 km S on Baños-Riobamba road, 2750 m, KU 141297; 10 km N Mocha, Puente de Mallo, 3079 m, UMMZ 132896(3), USNM 212036-38; 2 km S Mocha, 3000 m, USNM 212031-35; 10 km SW Mocha, 3700 m, KU 120018-21; 10-10.5 km SSW Mocha, 3450-3480 m, KU 179361-64; Patate, 16 km SSE, 2940 m, KU 141306, 16.5 km SSE, 2950 m, KU 141303-05, 17.1 km SSE, 2970 m, KU 141307-08, 20.6 km SSE, 3120 m, KU 141298-302; 3 km SSW San Miguelito, 2620 m, KU 131276-80; NW slope Volcán Tungurahua, 2730 m, KU 142132-34.

Eleutherodactylus myersi (20 spec.)

COLOMBIA, Depto. Cauca: Puracé highway, eastern slopes, 2900-3000 m, KU 143956; Puracé highway at San Juan Agua Terminales, 3000 m, KU 143954; 23 km E Puracé, 3275 m, KU 168432-35; 26 km E Puracé, 3130 m, KU 168436-38; 30 km E Puracé, 3030 m, KU 168439. Depto Nariño: ca. 4 km N Laguna de la Cocha, 3200 m, AMNH 86751-53; Páramo El Tábano, 3200 m, ICN 2503; 12 km E. Pasto, 3050 m, KU 168440-44; "20 miles east of Pasto," CAS 85177 (holotype).

Eleutherodactylus ocreatus (10 spec.)

ECUADOR, Prov. Carchi: El Pelado, 4150 m, MNHNP 03-217; W slope Volcán Chiles, 10 km W Tufiño, 3500-3800 m, KU 117573-81.

Eleutherodactylus orcesi (17 spec.)

ECUADOR, Prov. Bolívar: 5 km SW Bolívar-Chimborazo frontier, SW slope Nevado Chimborazo (= 24.8 km by road N Guaranda), 3800 m, KU 130314-16, 177814-16; 3 km W Bolívar-Chimborazo frontier, 3500 m, KU 130303; 21.7 km E Guaranda, 3410 m, KU 140003-04; 27.3 km E Guaranda, 3800 m, KU 140002. Prov. Chimborazo: 7.2 km WNW San Juan, 3160 m, KU 140001. Prov. Pichincha: 6-7 km W Chillogallo, ca. 3000 m, UMMZ 132903(4); Km 26 Quito-Chiriboga road, USNM 212039; 2 km E San Juan, UMMZ 132904.

Eleutherodactylus thymelensis (72 spec.)

COLOMBIA, Depto. Nariño: Mpio. Pasto, N slope Volcán Galeras, 3310 m, UVMP 2865-66.

ECUADOR, Prov. Carchi: El Pelado, 4150 m, MNHNP 03-218 á 220; Páramo del Ángel, 20 km SW Tulcán, 3350 m, KU 165944, ca. 23 km SW Tulcán, 3700 m, KU 117719-70; W slope Volcán Chiles, 10 km W Tufiño, 3500-3600 m, KU 117706-18. Prov. Pichincha: Km 224, Lago Agrio-Batán road (2.4 km W of crest), 3860 m, KU 177860.

Eleutherodactylus unistriatus (1346 spec. + 1 lot eggs)

COLOMBIA, Depto. Nariño: El Encano, 2630 m, ICN 1325-29, 4805-11; 7 km NE Guachucal, 3000 m, AMNH 86763-64, 86779; Guaitarilla, 2000 m, FMNH 54372, 54393-411, KU 138726-28; Laguna de la Cocha, 2800 m, AMNH 87874; Laguna de la Cocha, N shore, 2790-2850 m, AMNH 84853, 86765-77, KU 168587-617, 170148-49 (cleared and stained skeletons); 4 km N Laguna de la Cocha, 3200 m, AMNH 86762; Páramo El Tábano, 3200 m, ICN 2500; Municipio de Pasto, lado norte de Volcán Galeras, 3040 m, UVMP 2862; Pasto, Barrio San Fernando, LACM 50206-37; 8 km NE Pasto, 3020 m, KU 168567-83, 170147 (cleared and stained skeleton); 12 km E Pasto, 3050 m, KU 168584-86; west of Pasto, USNM 146220-35, 146238-47; Tangua, UVMP 2872; Tuqueres, FMNH 54373. Intend. Putumayo: Colón, 2220 m, KU 168618-24; 4 km SE San Francisco, 2320 m, AMNH 84837-38; Sibundoy, 2200 m, MCZ 56207-35, 58015-23.

ECUADOR, no other locality, MCZ 2261, 85082 (cotypes of *Phyllobates equatorialis*); "west Ecuador," BM 60.6.16.97/RR 1947.2.17.7-8, 60.6.15.105/RR 1947.2.17.9 (cotypes of *Hylodes unistriatus*). Prov. Carchi: Atal, near San Gabriel, 2700 m, UMMZ 83675(25), 83676(27), 83677(26), 92153(6), 92154(5); El Carmelo, 2710 m, KU 177521-28; 5.7 km NW El Carmelo, 2910 m, KU 177529-32; 10 km WNW El Carmelo, 3201 m, USNM 212064-67; Tulcán, 2770 m, KU 117623-36, 177472-512; 13 km SSE Tulcán, 3018 m, USNM 212051-52; 3 km S Tulcán, 2851 m, USNM 212053-63. Prov. Chimborazo: 1 km SW Guallabamba, 2860 m, KU 119750-92; 1 km S Guano, 2600 m, KU 131076; 8 km SE Licto, road to Alao, 3000 m, KU 141382-96; below Pungalá, at Río Alao, 2800 m, KU 141397-403; 1.6 km SE Pungalá, 3055 m, KU 141404-10; 8.2 km SE Pungalá, 3085 m, KU 141411-14; 8.5 km SE Pungalá, 3090 m, KU 141415-17; 11 km SE Pungalá, 3050 m, KU 131075; Riobamba, 2780 m, KU 119793; 15 km NW Riobamba, 3040 m, KU 165590. Prov. Cotopaxi:

Chillo (0°51'S, 78°34'W), 2745 m, MCZ 3023-27, 3034(3), UMMZ 47217; 2 km SE Lasso at Río Cotuchi, 2957 m, USNM 212068-69; Latacunga, 2750 m, KU 177515-17; 7 km E, 6 km S Latacunga, 2750 m, KU 127014; 1 km W Latacunga, 2750 m, KU 127015, 127024-30; Mulaló, 2990 m, KU 146124-35; 0.3 km N Mulaló, 3005 m, KU 141368; 1 km NE Mulaló, 3050 m, KU 127016-23, 127035-36 (skel.); 1 km S Mulaló, 3005 m, KU 141367; 0.3 km W Mulaló, 2980 m, KU 141366; Nudo de Tipulillo, El Chasquí, 3490 m, KU 130978; Pilaló, 2400 m, KU 143557, 177888-969; 11.3 km W Pujilí, 3500 m, KU 141369-71. *Prov. Imbabura:* Intag, BM 78.1.25.42 (cotype of *Hylodes buckleyi*); La Floresta, 2995 m, CAS-SU 9486-90; Laguna Cuicocha, 10 km W Quiroga, 2890-3000 m, KU 135351-92, 138788, 138125, 138832-51, 177513-14, MCZ 95546-54; Otavalo, 2550 m, KU 135397-427; near Otavalo, 2600 m, UMMZ 92152(11), 92155(8); 1 km N Otavalo, Quebrada San Miguel, 2650 m, KU 117638-47, 117666-67; 8 km NW Otavalo, 3100 m, KU 117698-705; 10-12 km NW Otavalo, 3300 m, KU 117674-97; 13-15 km NW Otavalo, 3300-3500 m, KU 117668-73; Quiroga, 2500 m, KU 135343-46; 7 km W. Quiroga, 2950 m, KU 135347-50; 4 km S San Pablo, NW slope Nudo de Mojanda, 3050 m, KU 131489-532; 6.9 km SE San Rafael, 2900 m, KU 180302 (lot of eggs); Urcusíquí, 12 km NW Otavalo, 3300 m, KU 117648-65. *Prov. Napo:* ca. 25-30 km SE Cayambe, 3190 m, CAS-SU 8280; Cotapino River (? locality), CAS-SU 10338(2); Santa Barbara, 2591 m, USNM 212070-72. *Prov. Pichincha:* 16 km W Aloag, 2810 m, KU 111132-35; 5 km W Aloag, N slope Cerro Corazon, 2945 m, KU 109066-67; 7 km W Aloag, 2810 m, KU 109068-69; 0.5 km N Cayambe, 2820 m, KU 130931-77; 6-7 km W Chillogallo, 3000 m, UMMZ 132905(4); Machachi, MCZ 3010, USNM

212138-48; region of Mindo, USNM 212150-51; Molino Urcu, AMNH 20139; 1 km E Nanegal Grande, 1524 m, UMMZ 132895(3); 2 km W Nono, USNM 212136-37; 9.5 km NW Nono, 2530 m, KU 165591-92; Pacto, USNM 212149; Quito, 2850 m, CAS-SU 2273, 2275-79, 10622-27, KU 94391, 111085-91, 138852-75, 152010-12, 177469-71, USNM 212073-79; 1.6 km ENE Quito, 2896 m, USNM 212132-33; 3.2 km ENE Quito, 2896 m, USNM 212134-35; 1.6 km SSE Quito, Río Machangara, 2744 m, USNM 212122-26; 2.4 km SSE Quito, 2744 m, USNM 212127-31; 2.4 km W Quito, SE slope Volcán Pichincha, 3500 m, USNM 212083-95; 1.6 km NW Quito, SE slope Volcán Pichincha, 3000 m, USNM 212080-82; 3.2 km NW Quito, 2988-3049 m, USNM 212096-121; San Juan, 3400 m, KU 177518-20; Volcán Pichincha, E. slope, 2900 m, KU 111092-131, 111136-37 (C&S skel.), 3480 m, KU 152013-25, 3390 m, KU 152026-31; S slope, 3480 m, KU 130979-80. *Prov. Tungurahua:* Ambato, 2700 m, KU 119794-800; Baños, 1900 m, CAS-SU 5083, UIMNH 55722, KU 141379-80; 5 km W Baños, 2439 m, USNM 212152-73; 7 km W Baños, 2805 m, USNM 212174-88, JAP 5938; 10 km W Baños, 2927-3049 m, USNM 212190-210; Chambo Grande, 7.6 km SE Pelileo, 2340 m, KU 141372, 141975-76, 146121-23; 10 km W Cotaló, 3300 m, KU 130897-930; 1 km W Juan Benigo Vela, 3080 m, KU 130981-89; Hda. Leito, Cerro Llangantí, 2439-2744 m, USNM 212189, 212211; 4 km N Mocha, 3140 m, KU 119801-04; 3 km SSW San Miguelito, 2620 m, KU 130990-1074, 131272-75; W slope Volcán Tungurahua (6.1 km SW jct. Río Pastaza and Baños-Riobamba road), 2470 m, KU 141373-74; W slope Volcán Tungurahua (13.2 km SW jct. Río Pastaza and Baños-Riobamba road), 2760 m, KU 141375-78; NW slope Volcán Tungurahua, 2730 m, KU 141977-85.

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